

MUTUALISTIC INTERACTIONS BETWEEN BIRDS AND FRUITS
IN A NORTHERN FLORIDA HAMMOCK COMMUNITY

By

STEWART T. SKEATE

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1985

ACKNOWLEDGEMENTS

It is my pleasure to acknowledge the many friends and colleagues who have aided me in this work. The members of my dissertation committee, John W. Hardy (chairman), Peter Feinsinger, Jack Kaufmann, and Walter Judd, provided helpful research and editorial suggestions. I should mention that this study is the result of a discussion question from Peter Feinsinger's community ecology class. I was also very fortunate to have the assistance of Edmund W. Stiles, Rutgers University, in the nutrient analysis of my fruits. I have also drawn heavily from Stiles' work on bird-fruit dispersal systems of North America. To Ted I extend my sincerest thanks. I also thank Doug White, Rutgers University, for providing me with invaluable manuscripts.

A number of post-doctoral associates and graduate students have helped me throughout my studies. I would especially like to thank Peter G. May, Nathaniel T. Wheelwright, and E.E. Spears for their help and suggestions.

I also acknowledge the Department of Zoology and the Frank M. Chapman Memorial Fund for their generous financial support. Thanks also go to the Florida Division of Natural Resources and the rangers of San Felasco Hammock State Preserve for their kind cooperation during the study. San

Felasco Hammock is truly a Florida jewel; I hope that this study adds to the understanding of this unique community.

I would like to separately thank my wife, Lea, for her field help and companionship. It was a joy for me to share the hammock with her. It will be a time and place we will always remember and cherish.

I must also thank my canine companion, Virgil. Through the miles and miles of walking, my wee westie was always there beside me (except when he was off chasing armadillos).

Finally, I would like to thank everyone I've been associated with at the Department of Zoology at UF for making my six year stay in Florida a wonderful experience.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	ii
LIST OF TABLES.....	v
LIST OF FIGURES.....	vi
ABSTRACT.....	vii
CHAPTERS	
ONE INTRODUCTION.....	1
Temperate Bird-Fruit Dispersal Systems.....	3
Nutritional Properties of Temperate Fruits.....	5
TWO SEASONAL PATTERNS OF FRUGIVORE AVAILABILITY AND FRUIT RIPENING.....	9
Study Site and Methods.....	9
Results and Discussion.....	14
Conclusions.....	56
THREE SEASONAL PATTERNS OF BIRD-DISPERSED FRUIT CHARACTERISTICS AND FRUIT REMOVAL.....	57
Methods.....	57
Results and Discussion.....	59
Conclusions.....	83
FOUR SUMMARY	86
APPENDICES	
I METHODS OF CALCULATING RIPENING SYNCHRONY.....	92
II FLOWERING AND FRUITING SCHEDULES OF BIRD- DISPERSED PLANTS OF SAN FELASCO HAMMOCK.....	94
III FRUIT TRAITS ANALYZED FOR BIRD-DISPERSED PLANTS OF SAN FELASCO HAMMOCK.....	98
IV BIRD-DISPERSED PLANT SPECIES AND THE BIRDS THAT FEED ON THEIR FRUITS AT SAN FELASCO HAMMOCK....	101
LITERATURE CITED.....	103
BIOGRAPHICAL SKETCH.....	111

LIST OF TABLES

Table 2-1. Fruit types of vascular plants found in San Felasco Hammock State Preserve, Florida.....	11
Table 2-2. Avian frugivores observed at San Felasco Hammock during censuses.....	15
Table 2-3. Observed frugivory by major and minor frugivores in San Felasco Hammock.....	17
Table 2-4. Resident status of avian frugivores at San Felasco Hammock.....	19
Table 2-5. Spearman rank correlation coefficients, r_s , for the relationship between frugivore species diversity and abundance and the number of plant species in fruit.....	31
Table 2-6. Relationship of mammal-bird fruits and bird-fruits to seasonal fruiting patterns.....	35
Table 2-7. Relationship of evergreenness to seasonal fruiting patterns for bird-dispersed plants of San Felasco Hammock.....	39
Table 2-8. Seasonal relationships of ripening characters for bird-dispersed plants of San Felasco Hammock.....	42
Table 2-9. Spearman rank correlation coefficients, r_s for ripening characters.....	43
Table 3-1. Relationship of fruit traits to seasonal fruiting patterns of bird-dispersed plants of San Felasco Hammock.....	61

LIST OF FIGURES

Figure 2-1. Number of frugivorous bird species observed along census route from April 1982 through May 1984 in San Felasco Hammock.....	21
Figure 2-2. Number of frugivore individuals observed along census route from April 1982 through May 1984 in San Felasco Hammock.....	24
Figure 2-3. Standard deviation of frugivore numbers for birds observed along census route from April 1982 through May 1984 in San Felasco Hammock.....	27
Figure 2-4. Number of bird-dispersed plant species with ripe fruit in San Felasco Hammock.....	30
Figure 3-1. Fall fruiting species. Percent of the initial total number of fruits removed within a single week for <u>Cornus foemina</u> , <u>Callicarpa americana</u> , and <u>Aralia spinosa</u>	71
Figure 3-2. Fall-winter fruiting species. Percent of the initial total number of fruits removed within a single week for <u>Viburnum rufidulum</u> , <u>Viburnum obovatum</u> , <u>Symplocos tinctoria</u> , <u>Ilex decidua</u> , <u>Smilax bona-nox</u> , and <u>Smilax</u> <u>auriculata</u>	73
Figure 3-3. Winter fruiting species. Percent of the initial total number of fruits removed within a single week for <u>Ilex opaca</u> and <u>Prunus caroliniana</u>	78

Abstract of Dissertation Presented to the Graduate
School of the University of Florida in Partial Fulfillment
of the Requirements for the Degree of Doctor of Philosophy

MUTUALISTIC INTERACTIONS BETWEEN BIRDS AND FRUITS
IN A NORTHERN FLORIDA HAMMOCK COMMUNITY

By

Stewart T. Skeate

August, 1985

Chairman: John W. Hardy
Major Department: Zoology

The ecological relationships between frugivorous birds and bird-dispersed plants have been unexplored at lower latitudes in North America. This paper examines interactions between 22 bird species and 45 species of bird-dispersed plants in a northern Florida hardwood hammock community from January 1982 to May 1984. Seasonal patterns of frugivore availability, fruiting phenology, and fruit characteristics were determined and compared.

Frugivore species diversity and abundance were highest during the fall and winter months and lowest in the spring and summer. Increases in frugivore numbers and diversity were attributed to the presence of migrant thrushes in the early fall and to overwintering frugivores in the late fall and winter. The number of fruiting species showed a significant correlation with frugivore diversity and

abundance. Spring and summer months showed the lowest number of fruiting species and fall and winter the highest, with a peak of 28 species in fruit in December.

Fruiting patterns of plant species fell into four seasonal groups: summer fruiting, fall fruiting, fall-winter fruiting, and winter fruiting. Nine species showed summer fruiting, bearing ripe fruit between early spring and late summer. Summer fruits were characterized by high water and carbohydrate content, large fruit mass, and low persistence. The 12 fall fruiting species ripened fruit at the peak of frugivore migration through northern Florida. Fall fruiting species were common or abundant in the community and included 5 species with high lipid fruits. The 20 fall-winter fruiting species produced highly persistent fruits that were available to migrant frugivores through fall and winter. These species were typically evergreen and included 5 species with high lipid fruits. The 4 winter fruiting species matured fruit in December and depended on overwintering birds for seed dispersal. All 4 species produced persistent, low lipid fruits.

The bird-fruit dispersal system of the lower temperate latitude hammock community shows similarities in fruiting patterns and fruit characteristics to middle latitudes of North America. Mild winters, the presence of evergreen species, and large populations of overwintering frugivores, however, have made winter fruiting more prevalent at lower latitudes compared to middle latitudes.

CHAPTER ONE INTRODUCTION

The importance of birds as seed dispersal agents for many plant species has long been recognized (Grinnell 1897, Proctor 1897, Ridley 1930, McAtee 1947, Krefting and Roe 1949). Nonetheless, only within the last ten years have researchers examined in depth the relationships between frugivorous birds and bird-dispersed plants. Early studies of bird-fruit interactions typically involved species records of birds that were observed visiting fruiting trees (Petrides 1942, Sutton 1951, Land 1963, Willis 1966, Leck 1969, Cruz 1974) and did not discuss possible mechanisms of bird-fruit relationships. Snow (1971) and McKey (1975) first speculated on possible coevolutionary trends between fruit-eating birds and plants, and presented a theoretical framework of bird-fruit relationships for future workers to investigate.

Bird-fruit interactions have also been of considerable interest to botanists from evolutionary, ecological, and morphological standpoints. Botanists agree that zoochorous seed dispersal has an ancient evolutionary history, probably originating in tropical environments (Corner 1964). The long history of bird-fruit interaction has resulted in distinct adaptations by fruits for dispersal by fruit-eating birds (Van der Pijl 1972). These include an attractive

edible portion, an outer protection against premature eating, an inner protection of the seed against digestion, colors that signal maturity, lack of odor, permanent attachment, absence of hard rind, and seeds exposed or dangling in hard fruits. These adaptations are highly variable among bird-dispersed plants. This is not surprising considering the widespread occurrence both geographically and taxonomically of fruits adapted for bird dispersal (Snow 1981, Wheelwright et al. 1984).

Recent field studies have examined various aspects of bird-fruit coevolution, including interactions between individual plant species and their dispersers (Howe 1977, 1980, 1981, McDiarmid et al. 1977, Howe and DeSteven 1979, Howe and Vande Kerckhove 1980, 1981, Herrera 1981b, Herrera and Jordano 1981); nutrient quality of fruit (Foster 1977, Stiles 1980, Sorensen 1981, Herrera 1981a, 1982b, Stapanian 1982, White and Stiles unpub. ms.); importance of fruit color and morphology to dispersal (Turcek 1963, Stiles 1982, Willson and Thompson 1982, Morden-Moore and Willson 1982, Denslow and Moermond 1982, Janson 1983, Willson and Melampy 1983, Levey, Moermond and Denslow 1984); relationship of seed dispersal to succession (Smith 1975, Thompson and Willson 1978, Debussche et al. 1982, McDonnell and Stiles 1983); importance of migrants as frugivores (Leck 1972, Hilty 1980, Rybczynski and Riker 1981, Greenberg 1981); the ecology of fruit-eating birds (Snow 1962, Crome 1975, Wheelwright 1983, Herrera 1984b); and the fruiting phenology

of bird-dispersed plants (Snow 1962, Thompson and Willson 1979, Herrera 1982b, 1984a, Wheelwright, in press).

These studies have spawned a "second generation" of review papers on the coevolution of seed dispersal systems (Stiles 1980, Wheelwright and Orians 1982, Howe and Smallwood 1982, Janzen 1983). These papers have contributed to the theoretical framework of bird-fruit research, but have also questioned existing theories on bird-fruit coevolution (see Wheelwright and Orians 1982). The field of seed-dispersal biology is in its infancy and lags behind other related fields such as pollination biology. Clearly more detailed field studies are needed in both tropical and temperate areas.

Temperate Bird-Fruit Dispersal Systems

The study of coevolved relationships between bird-dispersed plants and frugivorous birds in temperate regions has received considerable attention since Snow (1971) first discussed possible temperate fruiting patterns (Thompson and Willson 1979, Stiles 1980, Herrera 1981a,b, 1982a,b,c, 1984a,b, Herrera and Jordano 1981, Jordano 1982, Sorensen 1981, Stapanian 1982, Johnson et al. 1985). The relationship between the time of fruiting by bird-dispersed plants and frugivore diversity and abundance is basic to the understanding of temperate bird-fruit dispersal systems. Work by Thompson and Willson (1979) suggests that seasonal

patterns of frugivore presence may be the primary selecting force influencing mid-latitude fruiting patterns in North America. They recognized three mid-latitude fruiting patterns: summer, fall, and winter fruiting, in which the respective fruiting patterns showed distinct adaptations to differing levels of frugivore availability. Fall fruiting was the most common pattern, coinciding with the peak of avian frugivore migration.

To date, field studies of temperate bird-fruit dispersal systems in North America have been made at middle latitudes, north of the usual wintering grounds of most major avian frugivores (Sherburne 1972, Thompson and Willson 1979, Baird 1980, Johnson et al. 1985). The relationship between frugivorous birds and bird-dispersed plants at lower temperate latitudes in North America has been unexplored. Lower temperate latitudes differ from higher latitudes in their bird-dispersed flora and in seasonal diversity and abundance of frugivorous birds. This suggests that differences in fruiting patterns may be evident between middle and lower temperate latitudes in North America. Thompson and Willson (1979) suggest that both summer and winter fruiting patterns should be more profitable at lower temperate latitudes due to the greater availability of frugivores at the lower latitudes.

Few comprehensive field studies on bird-fruit dispersal systems at the community level exist (Sherburne 1972, Thompson and Willson 1979, Sorensen 1981, Herrera 1982a,

1984a,b). The majority of bird-fruit studies have involved dispersal strategies of individual plant species (e.g. Howe 1977, 1981, McDiarmid et al. 1977, Howe and Vande Kerchove 1980, 1981, Herrera and Jordano 1981, Jordano 1982). Studies dealing with single plant species may miss significant factors in the evolution or ecology of bird-fruit systems, factors that may be evident only through research at the community level (Herrera 1984a).

In this study I examine the bird-fruit system, involving 45 species of bird-dispersed plants and 22 frugivorous bird species, in a northern Florida hardwood hammock forest community. Four seasonal fruiting patterns are analyzed in the context of their relationship to frugivore availability, ripening synchrony, fruit abundance, habitat, and evergreenness. I also compare the bird-fruit systems of middle and lower temperate latitudes of North America in an attempt to derive a more complete picture of bird-fruit interactions in eastern North America.

Nutritional Properties of Temperate Fruits

The nutritional composition of fruits has been a major focal point in the study of temperate zone bird-fruit dispersal systems (Sherburne 1972, Stiles 1980, Sorensen 1981, Herrera 1982a, Stapanian 1982, Johnson et al. 1985, White and Stiles unpub. ms.). These studies have shown that temperate fruits exhibit wide variability in nutritional

content and that this is roughly related to seasonal ripening patterns. High reward fruits are produced during peak periods of frugivore availability, and the nutritional properties of the fruits are correlated with the seasonally changing demands of their major dispersers (Stiles 1980, Herrera 1982a, White and Stiles unpub. ms.).

Bird-dispersed plants are therefore under some selection pressure to produce fruits that are nutritionally attractive to frugivorous birds. By inducing birds to eat their fruits and then to regurgitate or defecate the seeds intact (see Snow 1971), plants obtain an effective method of seed dispersal away from the parent plant. This dispersal may result in lower seed and seedling mortality (Janzen 1970, Howe and Primack 1975), reduced seedling competition (Connell 1971, Harper 1977), increased gene flow (Levin and Kerster 1974), and dispersal to new habitats (Smith 1975). The nutritional reward offered by a plant in its fruit may also be related to the quality of seed dispersal by birds (Snow 1971, McKey 1975, Howe and Estabrook 1977, Howe and Vande Kerckhove 1980, but see Wheelwright and Orians 1982).

The actual nutritional reward in a fruit is determined by its dry mass content of carbohydrates, proteins or lipids. The latter two elements, however, appear to be the most important to frugivores (Snow 1971, Morton 1973, Foster 1977, Herrera 1982a). The presence of nutritionally irrelevant seeds in fruits, however, may influence the

attractiveness of a fruit. Therefore, in addition to the chemical (i.e. nutritional) properties, the structural or "design" features (Herrera 1982a) of a fruit may be important to a fruit-eating bird and may affect rates of fruit removal and digestive processing (White and Stiles, unpub. ms.). Structural fruit traits that may be important to birds include pulp moisture (Herrera 1982a), seed size and number (Sorensen 1984), taste (Stiles 1980, Sorensen 1983), fruit mass (Moermond and Denslow 1983), fruit diameter (Wheelwright 1985), presence of secondary compounds (Herrera 1982b), and fruit color (Turcek 1963, Morden-Moore and Willson 1982, Willson and Thompson 1982, Willson and Melampy 1983). Therefore, the attractiveness and profitability of any fruit to a bird is directly related to the combination of chemical and structural components of the fruit (Herrera 1982a).

The design and chemistry of fruits, by themselves, reveal relatively little about the evolution of bird-fruit dispersal systems. Only when this information is examined in the context of other community parameters can evolutionary patterns be discerned. Here, I report on fruit characteristics of 43 species of bird-dispersed plants in a northern Florida hammock forest community. Fruit characteristics analyzed are fruit mass, seed mass, total seed load, and water, lipid, protein, and soluble carbohydrate content. These characteristics should be important to fruit-eating birds from an energetic or

nutritional standpoint and have been analysed in other studies (Stiles 1980, Sorensen 1981, Herrera 1982a, White and Stiles unpub. ms.). I discuss the relationship of the nutritional content of fruits to seasonal ripening, fruit removal rates, frugivore availability, and fruit abundance. I also compare these results with the fruiting patterns described by Stiles (1980) and White and Stiles (unpub. ms.) for bird-dispersed plants of eastern North America. These studies have developed a framework for the study of bird-fruit dispersal systems for eastern North America and allow comparisons of fruit characteristics between middle and lower latitudes.

CHAPTER TWO
SEASONAL PATTERNS OF FRUGIVORE
AVAILABILITY AND FRUIT RIPENING

Study Site and Methods

Study Site

San Felasco Hammock State Preserve (29°45'N, 82°30'W), in Alachua Co., Florida, covers 2306 hectares and includes a variety of plant communities, including the largest protected stand of climax mesic hammock in the state of Florida (Dunn 1982). This area is characterized by moderate winters (15°-20°C average temperatures) and hot summers (30°C average temperature). Rainfall is variable in its seasonal distribution, although more than half the annual rainfall (average 1370 mm) occurs between June and September (Dohrenwend 1978).

This study focused on the mesic hammock community, which consists of 1294 hectares of rolling hills, plateaus, and stream valleys within San Felasco Hammock. The term mesic hammock refers to a mixed hardwood forest situated within a region where the predominant vegetation is prairie, marsh, or pine forest (Harper 1905). Mesic hammock is typically considered to be the climax vegetation of north central Florida (Harper 1905, Monk 1965, Veno 1976). Descriptions of the mesic hammock or southern mixed hardwood

community may be found in Laessle (1958), Monk (1965), and Delcourt and Delcourt (1977), while analysis of the plant communities and flora of San Felasco Hammock may be found in Ansley (1952) and Dunn (1982). Dominant canopy trees within this community include Quercus laurifolia, Q. virginiana, Carya glabra, C. tomentosa, Magnolia grandiflora, Persea borbonia, and Liquidambar styraciflua. The mixed deciduous-evergreen nature of this community is especially evident during the winter months, when the forest becomes a mosaic of evergreen and leafless broad-leaved trees. Plants with bird-dispersed fruits make up approximately one-half of the vascular flora of San Felasco's mesic hammock (Table 2-1). They are especially evident among shrubs, understory trees, and vines.

The Frugivores

I censused avian frugivore abundance and species diversity from January 1982 to May 1984 in the mesic hammock community. I walked three separate 700 m line transects twice weekly, one-half hour after sunrise, during which all birds seen or heard for 40 m to either side of the transect line were recorded. I determined 40 m to be an effective maximum distance for all seasons, particularly in the summer, when visibility was restricted due to vegetation. Although birds were more visible during the winter months, when many trees were leafless, the highly vocal nature of

TABLE 2-1. Fruit types of vascular plants found in San Felasco Hammock State Preserve, Alachua Co., Florida.

Life Form	Fleshy Fruits (%)	Dry Fruits (%)	Total Spp
Canopy Trees	4 (25)	12 (75)	16
Understory Trees	10 (67)	5 (33)	15
Shrubs	13 (93)	1 (7)	14
Vines	10 (63)	6 (37)	16
Herbs	4 (21)	15 (79)	19
Total Species	41 (51)	39 (49)	80

the birds during the summer months permitted an accurate census of their numbers. I combined data from the three transects to obtain a single daily count. Mean values of four daily transects over a two-week period were calculated, resulting in two values per month for abundance and species diversity.

Fruit-eating birds were determined to be so by direct observation during bird and fruit censusing. Only birds that swallowed entire fruits and that voided seeds intact were classified as frugivores. The term frugivore refers only to birds that disperse seeds (Snow 1971, Morton 1973). Birds that chewed fruits, swallowing only the fruit pulp and dropping the seeds below the parent plant, were considered "fruit-thieves" as they did not disperse seeds away from the parent plant (Howe and Estabrook 1977). I differentiated major frugivores from minor frugivores by the quantity of fruit eaten, the number of plant species visited, and the observed frequency of each species during weekly censuses.

The Plants

I collected phenological data on 45 bird-dispersed plant species in a 332 ha area of mesic hammock by monitoring ten individual plants per species when possible. Plant and bird censusing were made in the same area. In 1982-83, 486 plants of 44 species were tagged, whereas in 1983-4, 437 plants tagged were of 43 species. I recorded

dates of first ripe fruit and disappearance of all fruit for each individual.

I collected fruit ripening data for 27 species (24,238 fruits and 250 plants) in 1982-83 and for 23 species (12,390 fruits and 180 plants) in 1983-84. Weekly counts of ripe and unripe fruits were taken from tagged branches of ten plants per species when possible. I tagged approximately equal numbers of fruits for each individual of a particular species. The number of ripe fruits was corrected for fruit removed; I assumed that removed fruit were ripe. Prior to fruit ripening, I made fruit crop counts for each individual by direct count or extrapolation from fruit on a few branches and the total number of branches on the tree.

I analyzed ripening data by four measures: 1) between-plant ripening -- the number of days for all marked individuals to show 90% ripe fruit; 2) population ripening -- the number of days for the total fruit crop to reach 90% ripe fruit; 3) individual plant ripening -- the mean number of days for the marked individual plants of each species to reach 90% ripe fruit; 4) population synchrony index -- determined from a composite measure of individual synchrony. Individual synchrony measures the overlap of a given individual's ripening period (90% ripe fruit) with those of all individuals in the marked population. The method for calculating individual synchrony is presented in Appendix Ia. Population synchrony (Appendix Ib) is the synchrony of the mean individual with all other marked individuals in the

population. This measure of population ripening synchrony is a modification of Augspurger's method (1983) for determination of flowering synchrony.

I measured the abundance of the bird-dispersed plant species using a belt transect technique. I counted the number of individual plants of each species within 25 belt transects measuring 100 m X 10 m along a 2.5 km line transect through the study area. Only individuals judged to be capable of fruit production were counted. Fruiting species were then categorized as abundant, common, uncommon, or rare, based on their censused frequency, fruit crop size, and observed percentage of individuals fruiting within the population of each species.

In addition to fruiting records, I recorded flowering dates for the 45 bird-dispersed species by observation of plants within the study area. The flowering to fruiting duration was the time between the date of first flowering and the appearance of the first ripe fruit for each species.

Results and Discussion

The Frugivores

The frugivorous birds I observed in San Felasco Hammock from 1982 through April 1984 are listed in Table 2-2. Twelve of the twenty-two species were designated as major frugivores, based on the number of observations of fruit-eating

TABLE 2-2. Avian frugivores observed at San Felasco Hammock during censuses. Major frugivores are marked by asterisk.

	Code
Picidae	
Red-bellied Woodpecker (<u>Melanerpes carolinus</u>)*	1
Northern Flicker (<u>Colaptes auratus</u>)*	2
Yellow-bellied Sapsucker (<u>Sphyrapicus varius</u>)*	3
Pileated Woodpecker (<u>Dryocopus pileatus</u>)	4
Tyrannidae	
Acadian Flycatcher (<u>Empidonax virescens</u>)	5
Eastern Phoebe (<u>Sayornis phoebe</u>)	6
Sylviidae	
Ruby-crowned Kinglet (<u>Regulus calendula</u>)	7
Mimidae	
Brown Thrasher (<u>Toxostoma rufum</u>)	8
Gray Catbird (<u>Dumetella carolinensis</u>)*	9
Turdidae	
American Robin (<u>Turdus migratorius</u>)*	10
Veery (<u>Catharus fuscescens</u>)*	11
Wood Thrush (<u>Hylocichla mustelina</u>)*	12
Hermit Thrush (<u>Catharus guttatus</u>)*	13
Swainson's Thrush (<u>Catharus ustulatus</u>)*	14
Gray-cheeked Thrush (<u>Catharus minimus</u>)*	15
Eastern Bluebird (<u>Sialia sialis</u>)	16
Bombycillidae	
Cedar Waxwing (<u>Bombycilla cedrorum</u>)*	17
Vireonidae	
Red-eyed Vireo (<u>Vireo olivaceus</u>)	18
White-eyed Vireo (<u>Vireo griseus</u>)	19
Solitary Vireo (<u>Vireo solitarius</u>)	20
Yellow-throated Vireo (<u>Vireo flavifrons</u>)	21
Parulidae	
Yellow-rumped Warbler (<u>Dendroica coronata</u>)*	22

by these birds and by their observed frequency during the weekly censuses (see Methods). Thus the Eastern Bluebird (Sialia sialis), while showing a relatively high number of fruit visits, was not considered a major frugivore in the community as it was observed only twice in the study area during the two-year censusing period. Major frugivores accounted for 96.9% of the total observations of frugivory (one observation=one feeding bout) and 97.4% of the total visits (one visit=one fruit eaten) (Table 2-3).

Fruit thieves, birds that ate only the pulp of the fruit, dropping the seeds, included the Northern Cardinal (Cardinalis cardinalis), Summer Tanager (Piranga rubra), and Rose-breasted Grosbeak (Pheucticus cardinalis).

American Robins (Turdus migratorius) showed the highest number of fruit visitations among the major frugivores. Wintering robins were responsible for 57.2% of the total visits, while Cedar Waxwings (Bombycilla cedrorum) accounted for 19.8% of the total visits (Table 2-3). These figures are derived from the total number of visits over a two year period and may not reflect the importance of any single frugivore at one time of the year. Thus transient Veerys (Catharus fuscescens), while accounting for only 7.6% of the total visits, were the most important frugivores within the hammock community in the early fall prior to the arrival of Robins. Robins and wintering Hermit Thrushes (Catharus guttatus) visited the highest number of fruiting species, 18 and 16 respectively.

TABLE 2-3. Observed frugivory by major and minor frugivores in San Felasco Hammock, Florida. One observation=one feeding bout; one visit=one fruit eaten.

Bird	No. of Observations (%)	No. of Visits (%)	No. of Species
Major Frugivores			
Northern Flicker	30 (1.21)	306 (1.16)	5
Red-bellied Woodpecker	30 (1.21)	240 (0.01)	11
Yellow-bellied Sapsucker	22 (0.89)	268 (1.01)	9
Gray Catbird	19 (0.77)	180 (0.68)	6
Cedar Waxwing	342 (13.77)	5245 (19.79)	7
Veery	122 (4.91)	2023 (7.63)	5
Wood Thrush	34 (1.37)	317 (1.20)	4
Hermit Thrush	37 (1.53)	207 (0.78)	16
Swainson's Thrush	53 (2.13)	825 (3.11)	4
Gray-cheeked Thrush	18 (0.72)	158 (0.60)	2
American Robin	1556 (62.64)	15165 (57.22)	18
Yellow-rumped Warbler	142 (5.72)	889 (3.35)	3
Total	2406 (96.85)	25823 (97.43)	-
Minor Frugivores			
Pileated Woodpecker	8 (0.32)	120 (0.45)	5
Acadian Flycatcher	1 (0.04)	10 (0.04)	1
Eastern Phoebe	3 (0.12)	4 (0.02)	3
Ruby-crowned Kinglet	13 (0.52)	81 (0.31)	2
Brown Thrasher	7 (0.28)	73 (0.28)	5
Eastern Bluebird	19 (0.77)	260 (0.98)	1
White-eyed Vireo	4 (0.16)	37 (0.14)	3
Red-eyed Vireo	15 (0.60)	72 (0.27)	6
Solitary Vireo	6 (0.24)	16 (0.06)	3
Yellow-throated Vireo	2 (0.08)	7 (0.03)	1
Total	78 (3.14)	680 (2.57)	-

The number of frugivores in residence during each season is shown in Table 2-4. Only two major frugivores, the Red-bellied Woodpecker (Melanerpes carolinus) and the Wood Thrush (Hylocichla mustelina), were present in San Felasco Hammock during the summer. The Wood Thrush is a rare summer resident. The number of major frugivore species increased in the fall and winter; four were fall transients and five were winter residents. Migrants played a dominant role within the frugivore guild of this community. Migrants constituted 82% of the total number of frugivore species and 92% of the major frugivore species. Migrants were responsible for 98.2% of the total visits to fruiting plants, involving 30 plant species. Furthermore, the Eastern Bluebird (Sialia sialis) and Northern Flicker (Colaptes auratus), while year-round residents in northern Florida, appeared in the hammock community only during the fall and winter and were classified as "immigrants."

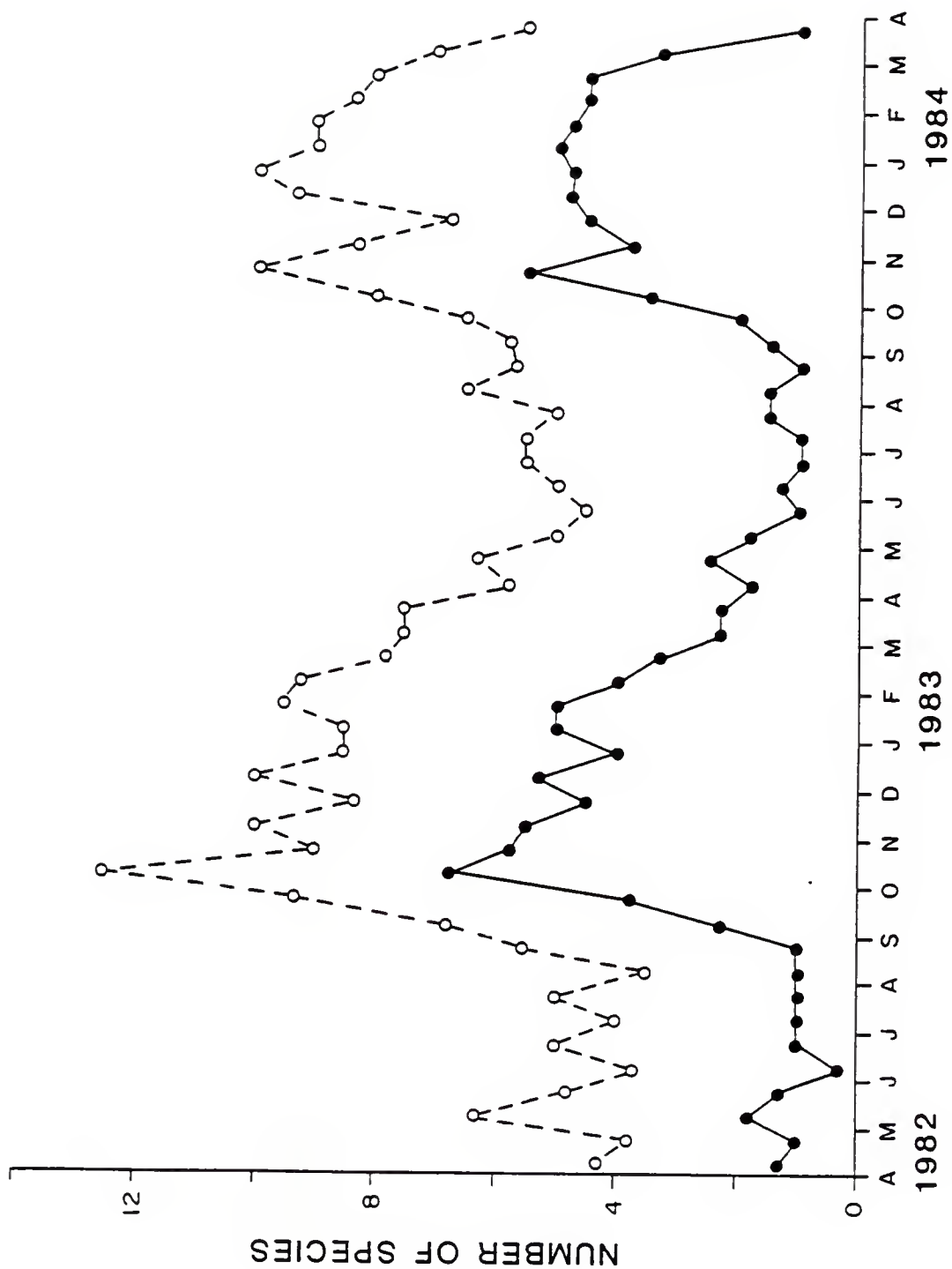
Frugivore Diversity and Abundance

Frugivore and major frugivore species diversity, which remained low throughout the summer months, increased in late September, reaching a peak in mid-October in both years (Fig. 2-1). This increase was due primarily to the arrival of migrant Veerys, Catbirds (Dumetella carolinensis), Swainson's Thrushes (Catharus ustulata), and Gray-cheeked Thrushes (Catharus minima). These migrants

TABLE 2-4. Resident status of avian frugivores at San Felasco Hammock, Florida.

	Year-round Residents	Summer Residents	Winter Residents	Fall Transients	Total
All Frugivores	4	4	10	4	22
Major Frugivores	1	1	6	4	12

Fig. 2-1. Number of frugivorous bird species observed along census route from April 1982 through May 1984 in San Felasco Hammock State Preserve, Alachua Co., Florida. The solid line represents major frugivores, the dashed line all frugivores (see text for details).



remained in San Felasco Hammock through October and departed at the end of the month. At this time, wintering Robins, Hermit Thrushes, Yellow-bellied Sapsuckers (Sphyrapicus varius), flickers, and Yellow-rumped Warblers (Dendroica coronata) arrived in the area. Frugivore species diversity remained high throughout the winter, decreasing from late March to early April, when the wintering frugivores left the hammock. Avian migration through San Felasco Hammock during the spring months was much less pronounced than fall migration, and frugivore diversity increased only slightly in the spring.

Frugivore abundance showed a pattern similar to that of frugivore species diversity: the number of frugivore individuals remained low during the summer months, increased in September, and reached a first peak in mid-October of both years (Fig. 2-2). A second peak was evident in both years, in mid-November in 1982 and mid-December in 1983. The first pulse of frugivore migration was due primarily to the arrival of migrant thrushes, while the second was due to the arrival of wintering robins, Cedar Waxwings, Hermit Thrushes, and Yellow-rumped Warblers. In 1982, robins arrived in large numbers in early November, while in 1983, large flocks of robins were not observed until mid-December. Cedar Waxwings were erratic in their occurrence as were Yellow-rumped Warblers.

The standard deviations of the four daily transects of frugivore numbers (see methods) for both years are shown in

Fig. 2-2. Number of frugivore individuals observed along census route from April 1982 through May 1984 in San Felasco Hammock State Preserve, Alachua Co., Florida. The solid line represent major frugivore numbers, the dashed line all frugivore numbers (see text for details).

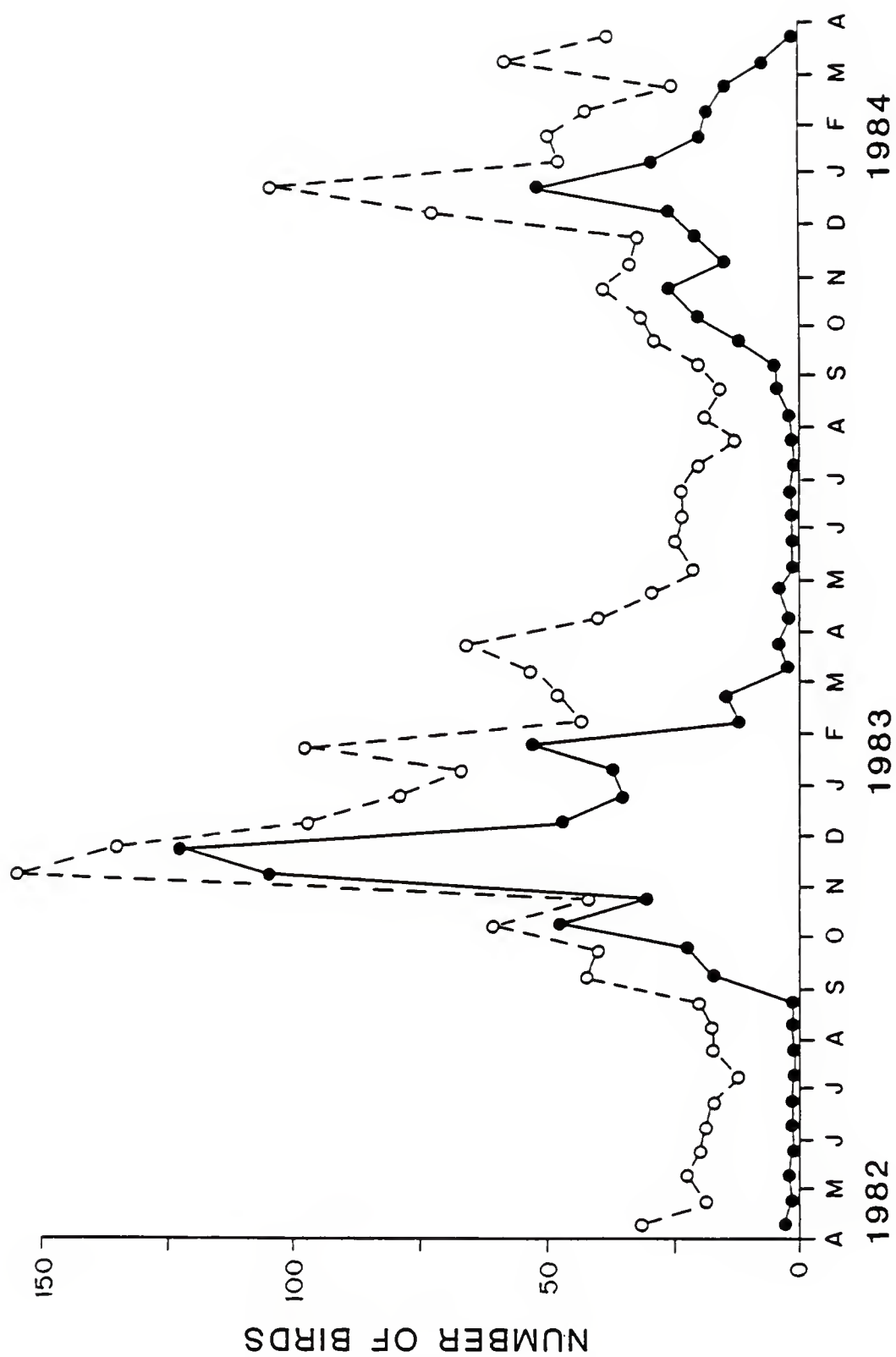
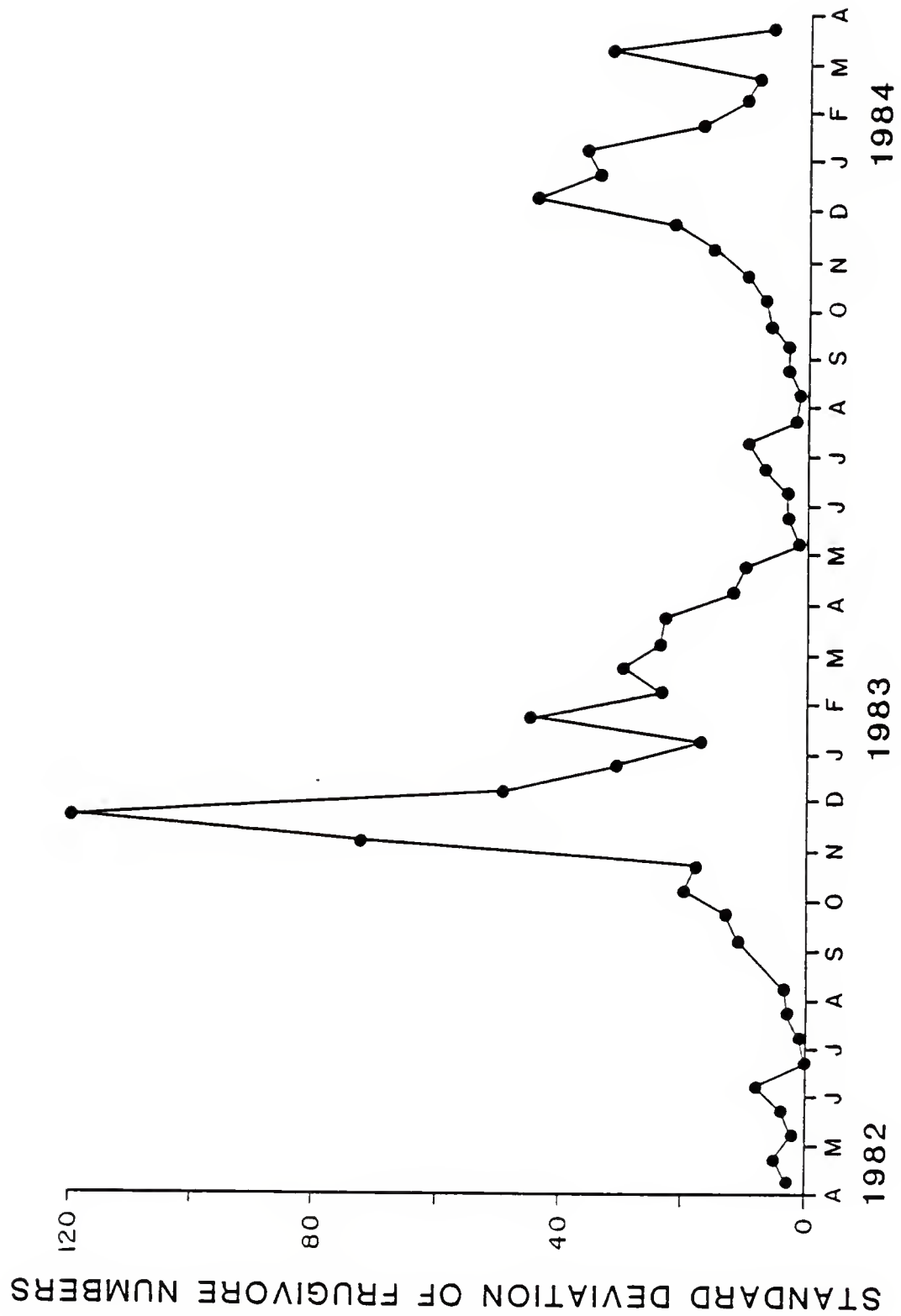


Fig. 2-3. Standard deviation values increased in early fall, reaching their greatest values in the late fall and early winter, while the summer months showed the lowest values. The high standard deviations evident in the late fall and winter months reflect the unpredictable nature of wintering frugivores as a resource for fruiting plants within the hammock community (Stapanian 1982).

There was no significant difference in major frugivore species diversity (Wilcoxon's Matched Pairs Signed-Ranks Test, $P > 0.05$) or frugivore species diversity (Wilcoxon's Matched Pairs Signed-Ranks Test, $P > 0.05$) between 1982-3 and 1983-4. There was also no significant difference in major frugivore abundance (Wilcoxon's Matched Pairs Signed-Ranks Test, $P > 0.05$) or frugivore abundance (Wilcoxon's Matched Pairs Signed-Ranks Test, $P > 0.05$) between the two years. However, there was a significant difference in major frugivore and frugivore abundance from September through March for the two years (Wilcoxon's Matched Pairs Signed-Ranks Test, $P < 0.05$), due to the higher number of frugivores observed in the fall and winter of 1982-83 compared to 1983-84 (see Fig. 2-2). I suggest that the lower numbers of wintering frugivores in 1983-84 were due to the small fruit crop of Cornus florida in 1983 (see below), which attracted fewer robins to the study site. In 1982-83, the mean flock size of robins was 18.2 ± 33.4 (range=1-250), while in 1983-84 the mean flock size was only 8.2 ± 13.7 (range=1-38). The presence or absence of robins appears to be partly related

Fig. 2-3. Standard deviation of frugivore numbers for birds observed along census route from April 1982 through May 1984 in San Felasco Hammock State Preserve, Alachua Co., Florida (see text for details).



to available fruit crops (Speirs 1946, Thompson and Willson 1979).

The Plants

The number of plant species with ripe fruits from April 1982 through March 1984 is shown in Fig. 2-4. The lowest number of species with ripe fruit occurred during the spring and summer. The number of species in fruit began to increase in late August and continued to increase through the fall, reaching a peak of 28 species in fruit in December. The number of fruiting species remained high throughout January, and began to decrease in February. There was no significant difference in the number of species in fruit per census period between 1982-3 and 1983-4 (Wilcoxon's Signed-Ranks Test, $P > 0.05$). There was a significant correlation between the number of fruiting species per census and major frugivore species diversity, frugivore species diversity, major frugivore abundance, and frugivore abundance (Table 2-5). There was a significant difference in the flowering to fruiting interval between summer fruiting and fall and winter fruiting species (Mann Whitney U-Test; $Z = 2.71$, $P < 0.01$). Because seasonal fruiting patterns are independent of seasonal flowering patterns, the ultimate timing of fruiting is apparently not a consequence of flowering time. Mean flowering to fruiting intervals

Fig. 2-4. Number of bird-dispersed plant species with ripe fruit in San Felasco Hammock, Alachua Co., Florida from April 1982 through May 1984.

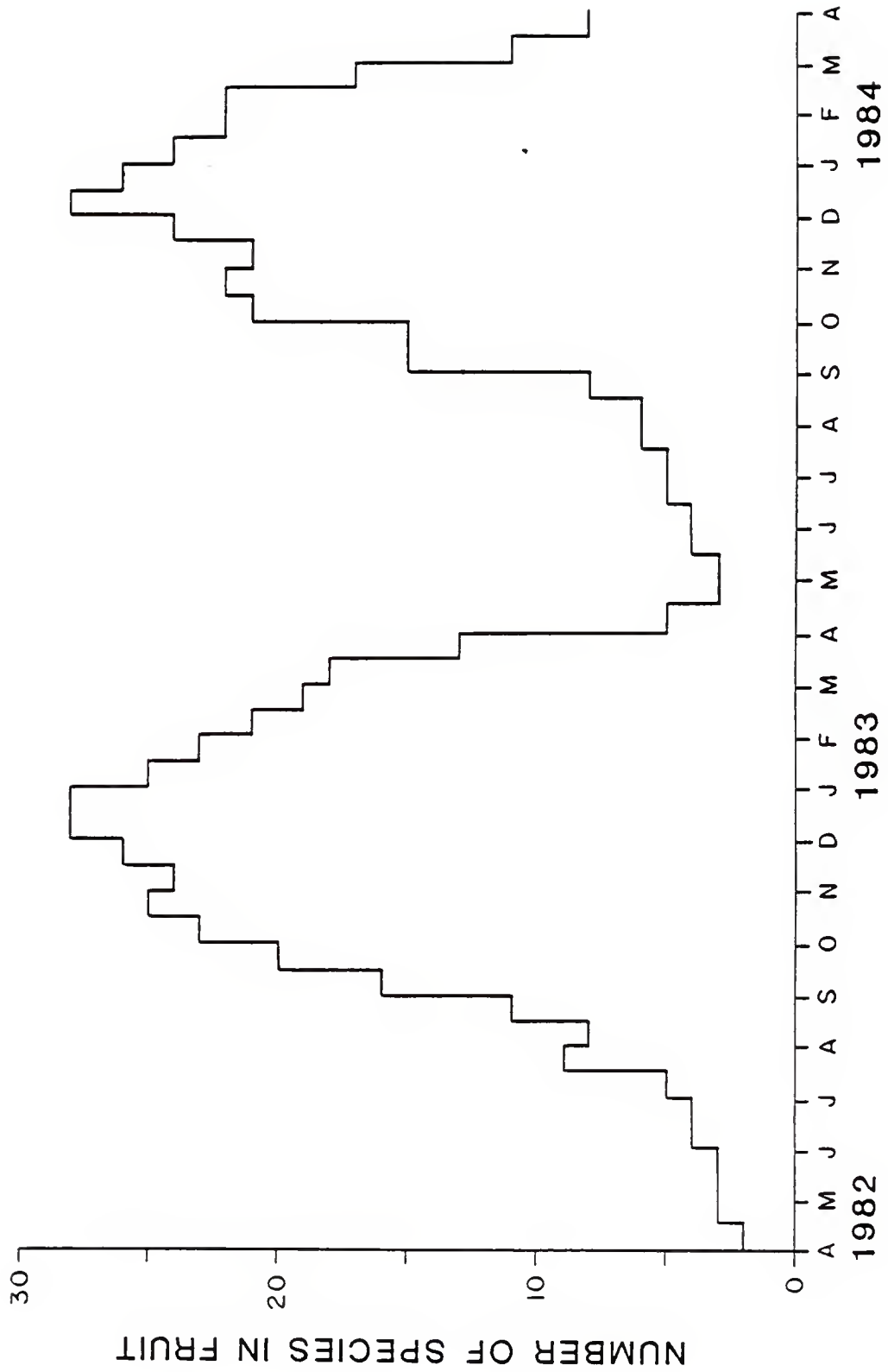


TABLE 2-5. Spearman rank correlation coefficients, r_s , for the relationship between frugivore species diversity and abundance and the number of plant species in fruit per two-week census period in San Felasco Hammock.

	1982-83	1983-84
	No. of Species in Fruit	No. of Species in Fruit
Major Frugivore Species Diversity	0.846**	0.784**
Frugivore Species Diversity	0.838**	0.841**
Major Frugivore Abundance	0.855**	0.879**
Frugivore Abundance	0.787**	0.673**

** $P < 0.01$.

were 78.4 d (N=9) for summer fruiting species and 142.1 d (N=36) for fall and winter fruiting species.

The majority of shrub and vine species produced ripe fruits annually, whereas a number of tree species only fruited heavily in alternate years or every three years. The latter fruiting behavior was evident in Cornus florida, Persea borbonia, and Nyssa sylvatica. Cornus florida had large fruit crops in 1982 but small crops in 1983, when isolated branches of individual trees produced flowers and fruits. Persea borbonia had large fruit crops in 1981, but very small fruit crops in 1982 and 1983, when only a few individuals produced fruit. Most Nyssa sylvatica individuals produced ripe fruits in 1981 and again in 1983, but only a few individuals bore fruit in 1982. The small fruit crop of Cornus florida in 1983 appeared to be a major factor in the lower number of frugivores seen in the fall of 1983 compared to 1982, when Cornus florida was a major source of fruit for a number of frugivore species. Persea borbonia may also affect frugivore abundance due to its potentially large fruit crops and lipid rich fruits. Shrubs that showed high annual variation in fruit crop size included Symplocos tinctoria, Ilex decidua, and Crataegus viridis.

Most plant species in 1983 produced ripe fruits within two weeks of their 1982 ripening dates. Species that ripened fruits later than the previous year also flowered later; thus the timing of flowering appeared to be an

important factor in the proximate timing of fruiting (see Appendix II). Symplocos tinctoria showed the greatest annual variation in ripening times, as this species ripened fruit in late July of 1982, but not until early October in 1983.

Fruiting Patterns

I have classified the 45 species of bird-dispersed plants in the hammock community into four seasonal fruiting patterns based on observed seasonal fruiting phenologies (see Appendix II). These include summer fruiting, fall fruiting, fall-winter fruiting, and winter fruiting.

Summer Fruiting

Nine species produced ripe fruit from early spring to late summer, before the arrival of fall migrants. Two subgroups were evident; Vaccinium myrsinites, Smilax smallii, Rubus cuneifolius, and Morus rubra had ripe fruit in the spring and early summer, while Chionanthus virginiana, Prunus angustifolia, P. serotina, Vitis aestivalis, and V. rotundifolia had ripe fruit in the late summer. The average fruiting duration for summer fruiting species was 64.9 d.

Most summer fruiting species have fruits characterized by a sweet taste and low persistence. These fruits appear to be adapted to attract mammals in addition to birds

(Stiles 1980). There is a decrease in the number of "mammal-bird" fruits from summer to fall to winter (Table 2-6). The predominance of mammal-bird fruits during the summer suggests that birds are unreliable seed dispersers at this time, and mammal-bird fruits may have evolved to increase the dispersal coterie of these plants. The unreliable nature of birds as dispersal agents during the summer is most likely due to their low abundance and diversity at this time and to their preference for abundant, protein-rich insects as a food source (Morton 1973).

Summer fruiting species consisted primarily of uncommon and rare fruiting species, with only two, Rubus cuneifolius and Vitis rotundifolia considered common in the study area. In contrast, 25 of the 36 fall and winter fruiting species were either abundant or common in the study area (see Appendix II).

Summer fruiting species typically occurred along second growth forest edge and in gaps within the forest. Only two summer species, Smilax smallii and Chionanthus virginiana, were found within the closed forest, whereas 28 of the 35 fall and winter fruiting species were forest inhabitants. Few frugivores visited second growth habitats in the hammock during the summer. The two major frugivores present during the summer, the Red-bellied Woodpecker and Wood Thrush, were forest residents and did not typically visit these habitats. The common breeding birds within these second growth habitats include cardinals and Rufous-sided Towhees (Pipilo

TABLE 2-6. Relationship of mammal-bird fruits and bird-fruits to seasonal fruiting patterns in San Felasco Hammock, Florida.

Fruiting Pattern	No. of Species	
	Mammal-Bird Fruits (%)	Bird Fruits (%)
Summer Fruiting	7 (77.8)	2 (22.2)
Fall Fruiting	1 (8.3)	11 (91.7)
Fall-Winter Fruiting	1 (5.0)	19 (95.0)
Winter Fruiting	0 (0.0)	4 (100.0)
Total	9	36

erythrophthalmus), which may be considered fruit-thieves or seed predators. However, I have observed cardinals "chewing" on these fruits and dropping the seeds intact, while feeding only on the pulp. If a cardinal moves the seed away from the parent plant, even a short distance, effective dispersal may result. Also, Thompson and Willson (1979) have found that while cardinals crush the large seeds of Lindera benzoin, the small seeds of Sambucus canadensis are passed unharmed.

Finally, the tendency of plants inhabiting disturbed habitats to fruit early may result from the importance of rapid reproduction and dispersal due to the colonizing nature of these plants. Such plants may reproduce upon reaching maturity, regardless of the time of year (Janzen 1967). Forest plants may not be under such constraints and may delay fruiting until the fall or winter.

Fall Fruiting

The 12 fall fruiting species (see Appendix II) yielded ripe fruits during September and October, at the peak of fall bird migration through northern Florida. The average duration of fall fruiting species was 74.1 d. Fruit disappearance typically occurred by January.

Fall fruiting species appear to exploit the first, more predictable pulse of frugivores in the early fall. Thompson and Willson (1979) suggest that this first wave is more

important than the second in the evolution of fruiting phenologies, due its greater predictability and higher species diversity. Certain fall fruiting species, such as Amelopsis arborea, Aralia spinosa, Cornus foemina, Magnolia grandiflora, Parthenocissus quinquefolia, and Phytolacca americana have their fruit dispersed almost exclusively by the first pulse, as their fruit crops are exhausted by the time the second wave arrives. Other fall fruiting species, including Cornus florida, Crataegus marshalli, Crataegus uniflora, Callicarpa americana, and Arisaema dracontium, still have fruit available for the second pulse.

Fall fruiting species are predominately "bird" fruits (Table 2-6), although Crataegus uniflora and Crataegus viridis, a fall-winter fruiter, appear to be adapted for dispersal primarily by mammals. These fruits exhibited poor persistence, often falling to the ground while still green. The ripe fruits are probably located by smell by ground foraging mammals.

Fall-Winter Fruiting

The fall-winter fruiting pattern was the most prevalent fruiting pattern in the hammock, occurring in twenty species. These species produced ripe fruits during the fall migration of frugivores that persisted through the fall into January and February. The average fruiting duration for fall-winter fruiting species was 150.8 d.

This fruiting pattern is synchronized with the first and second pulse of migrant frugivores. The highly persistent nature of these fruits may be an adaptation to the unpredictable nature of wintering frugivores in time and space (Stapanian 1982). Persistence may also be related to fruit quality and removal rates, as low quality fall-winter fruits show low removal rates (see Chapter III). Many of these species have ripe fruit in the fall, but do not have their fruits removed until January or February.

Fall-winter fruiting species consist of a higher proportion of evergreen species than summer or fall fruiting species (Table 2-7). The fruits of most evergreen species persist or ripen after the deciduous trees in the community have lost their leaves in late November.

The possession of persistent fruits or delayed fruit ripening in evergreen species may have a physiological basis, in that the evergreen condition allows for maintenance of persistent fruits or continued photosynthate buildup for maturing fruits. The abundant fall-winter fruit production in the scrublands of southern Spain has been attributed in part to the predominance of evergreen species within this community (Herrera 1982a, 1984a).

Evergreen species with persistent fruits are also clearly visible among the bare deciduous trees during the winter months. This is especially true for Persea borbonia, Smilax spp, Ilex opaca, Prunus caroliniana, Osmanthus americana, and Phoradendron serotinum. The persistent

TABLE 2-7. Relationship of evergreenness to seasonal fruiting patterns for bird-dispersed plants of San Felasco Hammock, Florida.

Fruiting Pattern	No. of Species	
	Deciduous	Evergreen
Summer; Fall Fruiting	18	3
Fall-Winter; Winter Fruiting	7	17
Total	25	20

Note - For 2x2 contingency: $\chi^2=12.3$, $P<0.005$

leaves of these species may act as foliar fruit flags (Stiles 1982), and avian dispersal agents may be attracted to trees with leaves as possible sources of fruit.

Winter Fruiting

The winter fruiting pattern was shown by four evergreen species (see Appendix II). In these species, fruit ripening did not occur until December, at which time the majority of wintering frugivores had arrived in Florida. The average fruiting duration of winter fruiting species was 87.8 d. These fruits showed high persistence and low spoilage. Important winter fruiting species included Prunus caroliniana and Phoradendron serotinum. Prunus caroliniana, a common tree along forest edges, provided an abundant food supply for wintering robins and woodpeckers, whereas Phoradendron serotinum constituted 70.5% of the total visits to fruiting plants by wintering waxwings. There was a close relationship between fruit ripening in Phoradendron serotinum and the arrival of waxwings at San Felasco Hammock. In 1982 and 1983, Phoradendron serotinum fruits ripened in mid-December, at which time waxwings were first observed in the area.

Winter fruiting species have large ripe fruit crops at a time when the majority of fall fruiting species are near fruit crop exhaustion and many of the fall-winter fruiters have reduced fruit crops. Winter fruiting species

provide wintering frugivores with low quality (see Chapter III) but abundant, concentrated fruits at a time when fruit supply is diminishing and frugivore metabolic needs are increasing due to colder temperatures. Delayed fruiting in winter fruiting species may also be an adaptation for the avoidance of competition for dispersal agents in the fall, when up to 32 species have ripe fruit.

Ripening Synchrony

There were no significant differences among the four seasonal fruiting patterns in between-plant ripening, population ripening, individual plant ripening, and population synchrony (Table 2-8). There was also no significant difference in these characteristics between the two years (Mann-Whitney U-test, $P > 0.05$). Between-plant ripening, population ripening, and individual plant ripening showed a significant positive correlation, while the index of population synchrony, Z , showed a significant negative correlation to between plant ripening, population ripening, and individual plant ripening (Table 2-9). Therefore, low Z values (low population synchrony) were associated with long asynchronous ripening periods (high between-plant ripening, population ripening, and individual plant ripening values).

The average between-plant ripening rates were 41.8 d (1982-83) and 36.2 d (1983-84); average population ripening rates were 33.5 d (1982-83) and 28.9 d (1983-84); average

TABLE 2-8. Seasonal relationships of ripening characters for bird-dispersed plants in San Felasco Hammock. 100/90%: time for 100% of marked individuals to show 90% ripe fruit; 90%: time for entire marked population to show 90% ripe fruit; $\bar{x}$ /90%: time for mean individual to show 90% ripe fruit; Z: index of population synchrony; N: number of species. Means and (SD) are shown.

Fruiting Pattern				
	Summer (d)	Fall (d)	Fall-Winter (d)	Winter (d) K-W Value*
1982-83				
100/90%	43.3(10.2)	43.0(24.9)	42.5(27.8)	34.0(12.1) 0.44 NS
90%	32.7(9.3)	37.5(27.2)	34.1(26.9)	23.3(4.0) 1.72 NS
$\bar{x}$ /90%	15.5(4.0)	20.5(18.8)	19.0(11.6)	15.5(7.9) 0.61 NS
Z	0.53(0.05)	0.58(0.27)	0.67(0.22)	0.66(0.16) 1.68 NS
N	3	6	15	3
1983-84				
100/90%	42.4(22.4)	37.0(25.0)	36.3(27.4)	18.5(16.3) 1.93 NS
90%	35.0(18.4)	30.3(15.5)	28.4(18.4)	14.5(10.6) 2.50 NS
$\bar{x}$ /90%	18.1(10.9)	11.5(1.9)	15.9(7.7)	8.1(1.5) 3.36 NS
Z	0.54(0.14)	0.54(0.22)	0.64(0.23)	0.88(0.18) 4.03 NS
N	5	3	13	2

*Kruskal-Wallis one-way analysis of variance. NS, not significant.

TABLE 2-9. Spearman rank correlation coefficients, r_s , for ripening characters. Correlation coefficients were calculated from 1983-84 data from Table 2-8.

	100/90%	90%	x90%	Z
100/90%	1.0000	-	-	-
90%	0.9705*	1.0000	-	-
$\bar{x}/90\%$	0.8662*	0.8524*	1.0000	-
Z	-0.6994*	-0.6936*	-0.5006*	1.0000

* $P < 0.05$

individual ripening rates were 19.5 d (1982-83) and 14.8 d (1983-84); and average population synchrony values were $Z=0.63$ (1982-83) and $Z=0.62$ (1983-84).

Individual species often differed greatly in the above characteristics. Between plant ripening rates ranged from 7 d (Smilax bona-nox) to 115 d (Symplocos tinctoria). Individual ripening rates varied from 7 d (Smilax bona-nox) to 39.3 d (Symplocos tinctoria). Population synchrony ranged from $Z=0.32$ (Symplocos tinctoria) to $Z=1.0$ (Smilax bona-nox).

The seasonal relationship of ripening synchrony suggested by Thompson and Willson (1979), in which summer fruiting species exhibit asynchronous between-plant ripening and fall fruiting species show synchronous between-plant ripening, was not evident for the northern Florida fruiting species. Herrera (1984a) also has found no obvious relationship between seasonality and ripening patterns in the bird-dispersed plants of the scrubland community in southern Spain. The extended availability of migrant frugivores at lower latitudes (September-November) may have resulted in less selection pressure for synchronous fall ripening compared to more northern latitudes in North America. This would be especially true for those species that use both fall pulses of frugivores. Those species that exploit only the first pulse of frugivores, however, including Aralia spinosa and Cornus foemina, do show a

tendency for synchronized ripening. Also, pronounced annual variation in ripening rates for a number of species suggests that proximate factors related to the physiology of fruit ripening may play an important role in the length of the ripening periods.

Middle and Lower Temperate Comparisons

The phenological patterns of northern Florida bird-dispersed plants and seasonal patterns of frugivore availability show a logical relationship with those patterns described by Thompson and Willson (1979) in Illinois. Frugivore diversity and abundance were highest in September in Illinois, while in Florida, highest values occurred in October. The month-long difference would reflect the movement of migrant frugivores from middle to lower latitudes. The two September peaks in frugivore diversity and abundance in Illinois correspond to the two peaks evident in northern Florida in October and November. The first peak in both areas consisted primarily of thrush species, while the second pulse consisted of robins, Hermit Thrushes, and Yellow-rumped Warblers.

The number of species in fruit in Illinois begins to increase in August, reaching peaks in late August and September. In northern Florida, meanwhile, fruiting species diversity begins to increase in September, reaching peaks in October, November, and December. The fruiting peaks in

both areas correspond to periods of high frugivore availability. It is likely that, as migrant frugivores pass from upper to middle to lower latitudes in North America, they encounter peaks of fruit production at each latitude.

As predicted by Thompson and Willson (1979), the winter fruiting strategy at lower temperate latitudes in North America is more pronounced than at middle or upper latitudes. Twenty-four species of plants have ripe fruit during the winter months in the hammock community, compared to only four species in Illinois. High frugivore availability, mild winters, and the presence of evergreen species have made winter fruiting possible and profitable in northern Florida. Low frugivore abundance, cold winters, and the dominance of deciduous species restrict winter fruiting to only a few species at northern latitudes.

The second prediction of Thompson and Willson (1979), that summer fruiting should be more profitable at lower temperate latitudes, is not supported by this study. The absence of major frugivores, abundance of insects, and potential problems with microbial spoilage apparently have restricted summer fruiting to a relatively few species, which may depend more on mammals for dispersal than on birds. I suggest that the summer fruiting strategy should be more profitable at more northern latitudes, where breeding robins and thrush species are abundant. The importance of fruits in the diets of juvenile robins and thrushes has not been studied in detail, although anecdotal

accounts of adult thrushes feeding fruits to their young do exist (see Bent 1949).

Lower Temperate Latitude Dispersal Systems

Possibly the most thorough single community analysis of bird-fruit coevolution to date has been made in the scrublands of southern Spain (Herrera 1981a,b, 1982a,b,c, 1984a,b, Herrera and Jordano 1981, Jordano 1982, Jordano and Herrera 1981). Similarities between Florida and southern Spain in seasonal frugivore availability make a comparison of the bird-fruit system in these two areas worthwhile. Southern Spain is a major flyway in the fall for transient avian frugivores migrating south to wintering grounds in Africa, while during the winter it is home to a number of overwintering frugivores (Herrera 1982a, 1984a). As this is an analogous situation to that in Florida, it is logical that similar phenological strategies related to dispersal should be evident for the bird-dispersed plants in these two regions.

Fruit-eating by birds in the scrubland community of southern Spain appears to be limited to passerine species (Herrera 1984a,b), whereas in the Florida hammock community four woodpecker species are significant consumers of fruit. Fruit-eating among the scrubland passerines is widespread: approximately 67% of the passerines within this community eat fruit (Herrera 1984a), compared to approximately 56% of

the passerine species in the hammock community. Fruit predators are also more prevalent in the scrublands, where 69% of the fruit-eating birds are considered fruit predators, while only three species of fruit predator were observed in the hammock community.

As does the hammock community, the scrublands has a subset of major frugivores, consisting primarily of fall migrants and overwintering species, that is responsible for most of the frugivory within the community (Herrera 1984a). The major frugivores in the Spanish scrublands tend to be smaller, 12-18g body mass (Herrera 1984a,b) than those in Florida (40-100g body mass) and other North American forests (Sherburne 1972; Stiles 1980; Rybczynski and Riker 1981). Herrera (1984a) has attributed the absence of large frugivores in this community to possible difficulties in foraging for fruit in the dense scrub and to the prevalence of fruiting displays involving thin stems and erect infructescences.

The Spanish scrubland community shows a proportion of bird-dispersed plant species, 49-66% (Herrera 1984a) similar to that in the hammock community (approximately 50%). The presence of resident, transient, and overwintering frugivores in southern Spain and Florida has resulted in the availability of fruit during every month of the year for both communities. Most plants in both communities, however, bear ripe fruit in the fall, when migrant frugivores arrive. Herrera (1982a, 1984a) has

attributed the prevalence of fall-winter fruiting in the Spanish scrublands to the high degree of evergreenness and mild winters that are characteristic of this community. This is a similar situation to that in the hammock community, where mild winters have allowed the establishment of such subtropical evergreen species as Magnolia grandiflora, Persea borbonia, Symplocos tinctoria, Osmanthus americanus, and Prunus caroliniana.

Herrera (1984a) maintains that the scrubland bird-plant dispersal system during fall and winter is driven by relatively few pairs of strong reciprocal primary plant-bird interactions (e.g. Pistacia lentiscus-Sylvia atricapilla; Viburnum tinus-Erithacus rubecula). These highly nutritious primary plants indirectly favor seed dispersal of low-reward or rare coexisting plants due to the varied diets exhibited by the primary frugivores. Thus the plant species interact via diet-sharing and form an interdependent dispersal guild (Herrera 1984a).

There is also good evidence for the presence of primary plant-bird interactions in the northern Florida hammock community. In the early fall, when the Veery is the primary visitor to these plants, Parthenocissus quinquefolia and Aralia spinosa are the most frequently visited plants in the community. Parthenocissus quinquefolia is a high lipid fruit (see Chapter III), and Aralia spinosa, while low in lipids, is a common, highly visible plant within the community, offering an abundant fruit crop. Later in the fall, after

Parthenocissus and Aralia fruit crops are exhausted, there is a close relationship between Veerys and Cornus florida, another high lipid fruit. In November, after Veerys leave the area, robins become the primary dispersal agent in the hammock community. During late fall and winter, robins sequentially become the primary dispersal agent for a series of fruiting plants, including Cornus florida, Persea borbonia, and Prunus caroliniana. At these times, while the majority of visits by robins are to these primary plants, they also visit 15 other fruiting plant species.

A similar situation exists for the Cedar Waxwing and the mistletoe, Phoradendron serotinum. The presence of mistletoe fruits, the waxwing's principal food within this community, attracts the highly frugivorous waxwing to the hammock community, where it feeds on 7 fruiting species.

It does appear, therefore, that the bird-dispersed plants of the hammock community form a dispersal guild, dependent on a relatively few species of lipid-rich or abundant fruiting species. This dispersal guild is in turn dependent on a few species of abundant frugivores (e.g. Veerys and robins). The temporal sequence of primary plants ensures frugivore abundance throughout the fall and winter months and suggests possible temporal partitioning in fruiting among the primary plant species. The importance of these primary plant species was evident in 1983, when Cornus florida and Persea borbonia had small fruit crops. Frugivore abundance, including the number of robins, was

significantly lower than in 1982, when Cornus florida showed a large fruit crop.

Despite the similarities in fruiting patterns between the hammock and scrubland communities, climatic and physiognomic differences limit comparisons between these two communities. The Spanish scrublands receive approximately one-half the annual rainfall of the hammock community and have a drier summer. Also, the scrublands have a continuous distribution of fruit-producing low shrubs (Herrera 1984a), while the hammock community has a patchy distribution of fruiting trees, shrubs, and vines. Community analysis of bird-fruit interactions in the southern California chaparral community of North America should show patterns more similar to those found in the Spanish scrublands, due to the similarity in the climate and vegetation of the two areas.

Historical Considerations

It is likely that mesic hardwood communities were present in northern Florida throughout the Pleistocene, when this area acted as a possible glacial refuge for northern deciduous trees (Delcourt and Delcourt 1981). Glaciation over the past 80,000 years appears to have had a more pronounced effect on middle and upper temperate North American latitudes than on lower latitudes. Warm temperate oak-hickory-pine forests dominated at lower latitudes during

glacial periods compared to the boreal vegetation of the middle and upper temperate latitudes (Delcourt and Delcourt 1981).

The Quaternary glaciations also have had a major influence on avian migration patterns and are responsible for the current geography of avian migrations (Dorst 1962). It is likely that northern Florida, with its mild climate and mesic hardwood forests, served as a refugium for many North American bird species during the glaciations. The Atlantic coast flyway migration route (Lincoln 1939) channels avian migrants from most of eastern North America through northern Florida on their way to wintering grounds in Central America, South America, and the West Indies. The predictable pulse of fall migrants, the mild winters of northern Florida, and the established southern mesic hardwood forest community have provided the raw materials necessary for the evolution of mutualistic interactions between fruiting plants and fruit-eating birds in the southern mixed-hardwood community.

No discussion on the evolution of eastern North America forest community structure would be complete without mention of the extinct Passenger Pigeon, Ectopistes migratorius. It was once extremely abundant in deciduous forests from the great plains to the Atlantic coast of New Brunswick, wintering throughout the southeastern states (Schorger 1955). The Passenger Pigeon's diet consisted primarily of mast, including acorns, beechnuts, and

chestnuts, but they were also known to feed upon a variety of fruits, including Prunus spp., Ilex spp., Nyssa sylvatica, Cornus florida, Morus spp., Rhus spp., Mitchella repens, Phytolacca americana, Myrica cerifera, Vitis spp., and Aralia spinosa (Schorger 1955). It is likely that Passenger Pigeons were effective dispersal agents for the majority of these fruits, voiding the seeds intact. Nonetheless, we do not know the relative importance of fruit compared to mast in the Passenger Pigeon's diet.

The southernmost limit of the Passenger Pigeon's wintering range in Florida has been listed as Alachua Co., where it was reported to be abundant in the eighteenth century (Howell 1932). The primary ecological role of the Passenger Pigeon was probably that of a seed predator of mast-producing species. However, due to the inclusion of fruit within its diet and its large numbers, it is possible that the Passenger Pigeon played a significant role in the evolution of the bird-fruit dispersal system in eastern North America. Thus, its presence in northern Florida during the winter may have in part selected for the predominance of fall-winter fruiting in this area.

Numbers of the American Robin, the primary wintering frugivore in northern Florida today, seem to have increased due to the clearing of forests in its breeding grounds (Stiles pers. comm.). Nonetheless, it is likely that robins have been a major force in the coevolutionary relationships between fruiting plants and frugivorous birds in northern

Florida. This would be especially true in the selection for fall-winter fruiting, as the primary wintering ground for robins is Florida, where flocks of up to 50,000 have been recorded (Speirs 1953).

Phytogeographic Considerations

The bird-dispersed flora of San Felasco Hammock shows strong taxonomic affinities with the mid-latitude flora of eastern North America. Of 22 plant families represented in San Felasco Hammock, only 2, *Palmae* and *Symplocaceae*, are confined to the southeastern United States in their U.S. distribution. At the generic level, of 31 genera represented in San Felasco Hammock, only 8, Amelopsis, Callicarpa, Chionanthus, Osmanthus, Persea, Phoradendron, Sabal, and Symplocos, are restricted primarily to the southeast. At the species level, however, 29 of the 45 species present at San Felasco Hammock (64.4%) are limited to the southeast. Twenty-four of these species bear ripe fruit in the fall or winter. Therefore, at the species level, the bird-dispersed flora of lower latitudes is distinct from the flora of mid-latitudes of eastern North America. Yet many of the species confined to the southeast have congeners at more northern latitudes that show similar life forms and fruiting displays (e.g. species of Viburnum, Ilex, Smilax, Crataegus, Celtis, Cornus, Vaccinium). Only six species, Sabal minor, Prunus caroliniana, Phoradendron

serotinum, Persea borbonia, Magnolia grandiflora, and Symplocos tinctoria, show strong tropical affiliations. This contrasts with the bird-dispersed flora of southern Florida, where tropical elements comprise approximately 87% of the bird-dispersed plant species (Tomlinson 1980).

Certain taxa show wide variation in fruit types and phenology, while others are quite uniform. Prunus angustifolia, P. serotina, and P. caroliniana, while all flowering in early spring, show pronounced differences in fruiting phenology. Prunus angustifolia and P. serotina bear ripe fruit in the summer, while P. caroliniana ripens fruit in December. Also, while P. angustifolia produces a sweet mammal-bird fruit that shows low persistence, P. caroliniana produces a bitter bird-dispersed fruit that is highly persistent. Evergreenness is a good indicator of phenological patterns: the deciduous species, P. angustifolia and P. serotina, are summer fruiterers, while the evergreen, P. caroliniana, is a winter fruiter. This latter situation also exists for two species within the Oleaceae, Chionanthus virginianus and Osmanthus americanus. The deciduous C. virginianus shows summer fruiting, while the evergreen O. americanus is a winter fruiter.

Within certain genera such as Smilax and Ilex, however, different species tend to exhibit similar fruiting patterns, similar fruit types, and highly persistent fruits. It is difficult to determine, however, if similarities within these genera in fruiting patterns are the result of

taxonomic constraints or the result of similar selective pressures acting on each species. The relationship between systematics and ecological adaptation is complex and may be indirect, and the effects of evolutionary canalization must be considered in analyzing the biological interactions of each taxon (Stebbins 1974).

Conclusions

The strong similarity in the bird-dispersed floras of lower and mid-temperate latitudes in eastern North America has probably played an important role in the evolution of the bird-fruit seed dispersal system that we see today. Wide-ranging species, such as Parthenocissus quinquefolia and Cornus florida, supply migrating frugivores with a continuous, familiar food supply in time and space along the Atlantic flyway, while congeners in the south show fruiting displays to migrating frugivores similar to those of their relatives in the north. Thus throughout eastern North America there is a continuity in both the floral and frugivorous components of the bird-fruit dispersal system. Add to this the highly predictable nature of the annual fall migration of avian frugivores from upper to lower latitudes, and it is not suprising that we see phenological patterns of fruit ripening that are consistent with frugivore migration and availability.

CHAPTER THREE
SEASONAL PATTERNS OF BIRD-DISPERSED
FRUIT CHARACTERISTICS AND FRUIT REMOVAL

Methods

Fruit Samples

I collected ripe fruits from 38 bird-dispersed plant species in San Felasco Hammock. Fruit mass, seed (or pyrene) mass, pulp yield, and water content were determined from an aggregate sample of 3474 undamaged fruits (mean = 91.4). Fruits were counted, weighed, and separated into pulp and seed components by dissection with forceps and by hand. Pulp and cleaned seeds were weighed, and the pulp was oven-dried to constant mass at 60°C. All masses were measured to the nearest 0.1mg on a Mettler AK 160 scale. I defined pulp moisture as percent mass lost on drying separated pulp. Total dry pulp per fruit was determined from the mass of wet pulp (fruit mass minus the mass of clean seeds) and its moisture content. I determined individual seed mass from wet seed load per fruit and mean number of seeds per fruit for each sample.

Pulp samples were frozen and stored until shipped to the Rutgers University Fruit Lab, where they were analyzed under the supervision of Dr. E.W. Stiles. Lipid content was determined to be percent mass lost in 16-18h extraction with

petroleum ether in Micro-Soxhlet apparatus. Protein content was estimated as 6.25 times nitrogen found by micro-Kjeldahl extraction (Association of Official Agricultural Chemists 1965), and soluble carbohydrate content was determined by the anthrone method (Yemm and Willis 1954; Allen 1974). Results for each chemical test are mean percent of dry mass from analysis of two subsamples. In addition to the 38 species of fruits collected from San Felasco Hammock, I have included in my results analysis of 5 species (Morus rubra, Rubus cuneifolius, Prunus serotina, Ilex glabra, and Toxicodendron radicans) from samples collected in New Jersey and analysed by White and Stiles. These species occur in San Felasco Hammock, but I was unable to collect sufficient numbers of fruits for analysis due to their scarcity or inaccessibility. The nutritional composition of species of Morus, Rubus, Prunus, and Ilex have been shown to be consistently similar (see Stiles 1980, White and Stiles unpub. ms.). I have therefore included figures from the New Jersey samples in my seasonal analyses. I have omitted Toxicodendron radicans from my statistical comparisons as consistent nutritional patterns are not evident for this genus as compared to the other genera.

Removal Rates

I determined weekly rates of fruit removal for 11 species of bird-dispersed plants involving 125 individuals

and 13,902 fruits in 1982-83, and for 8 species, involving 74 individuals and 6,334 fruits, in 1983-84. Weekly counts of fruits on tagged branches of marked plants were made. I also tagged additional branches of marked plants each week to replace removed fruits. This was done in an attempt to maintain a constant number of marked fruits for each individual for each week. I defined removal rate as the percentage of the total marked population of fruit removed within a seven-day period.

I obtained additional information on fruit removal by direct observations of fruit-eating birds. I made records of fruit-eating while walking a 2100m transect 2 mornings each week during bird censuses (see Chapter II) and during fruit censusing from January 1982 to April 1984.

Results and Discussion

Fruiting Patterns

The 43 species of bird-dispersed plants of San Felasco Hammock fall into four fruiting patterns: summer fruiting, fall fruiting, fall-winter fruiting, and winter fruiting (see Chapter II). These fruiting patterns are based only on seasonality of fruiting; a single fruiting pattern may include species with different life forms, fruit types, and dispersal strategies. Nonetheless, evergreenness, habitat

preference, and fruit abundance are related to fruiting seasonality.

Summer Fruiting

Summer fruits (9 species) of the hammock community are characterized by a large fruit mass, low seed load, high water content, low lipid and protein content, and high carbohydrate content (Table 3-1). Summer fruits include 7 species that depend on both mammals and birds for seed dispersal. These "mammal-bird" fruits are characterized by low persistence (fall to the ground upon ripening), high sugar content, and a sweet taste (Stiles 1980). Morus rubra, Rubus spp., Vitis spp., Vaccinium spp., and Prunus spp. (but not P. caroliniana) are eaten on a regular basis by a number of mammals, including raccoons and skunks (Martin et. al. 1951). The production of fruits that are attractive to mammals may be advantageous due to the low availability of avian frugivores during the summer months. Fruit use by breeding birds is probably also reduced due to the abundance of insects at this time and the importance of insects as a high-protein food for breeding birds (Morton 1973).

Stiles (1980) has suggested that a dichotomy in seed size, perhaps related to susceptibility to seed predation by mammals, exists for summer fruits with mixed bird and mammal dispersal. Small-seeded species produce seeds that may pass

TABLE 3-1. Relationship of fruit traits to seasonal fruiting patterns of bird-dispersed plants of San Felasco Hammock, Florida. Means (1 SD) are shown.

Fruit Trait	Fruiting Pattern				F. Value ⁺
	Summer	Fall	Fall-Winter	Winter	
Fruit Mass (mg)	1036.5(913.5)	282.3(199.5)	251.8(256.3)	426.2(279.8)	6.4**
Seed Mass (mg)	94.4(126.4)	38.4 (36.6)	98.0(182.9)	154.6(170.3)	0.7NS
Seed Load (%)	20.4(16.5)	26.3(12.0)	40.7(16.4)	32.4(17.3)	4.0*
Dry Pulp (mg)	105.8(96.6)	52.4(40.1)	50.1(44.8)	80.1(47.9)	2.1NS
Water (%)	82.7(7.1)	73.4(15.6)	55.4(25.1)	67.2(8.0)	5.8**
Lipid (%)	1.9(1.2)	20.5(21.5)	6.3(11.7)	2.1(2.9)	2.9*
Protein (%)	3.6(2.1)	3.9(2.4)	4.6(3.0)	5.8(4.0)	0.8NS
Carbohydrate (%)	57.2(11.0)	37.0(22.5)	37.0(18.9)	48.6(8.4)	3.1*
No. of Species	9	11	19	4	

⁺ F values were computed after arcsin transformation for percentage data.
 * P < .05; ** P < .005

through the guts of small mammals undamaged, while the large-seeded species may produce seeds so large as to discourage seed predation by small mammals. Hammock mammal-bird fruits separate into small-seeded species (mean seed mass = 1.53 ± 0.80 mg, $n=3$) and large-seeded species (mean seed mass = 241.70 ± 116.79 mg, $n=3$). The small-seeded species also show very low seed loads (mean seed load = 8.2%).

Two summer fruiting species, Prunus angustifolia and Vitis rotundifolia, produce large fruits (> 2000mg) that are clearly too large to be swallowed by any resident bird. Mammal-dispersed fruits have been characterized by a large size and an orange or yellow color (Janson 1983, White and Stiles unpub. ms.). Prunus anugustifolia and Vitis rotundifolia, however, produce purple fruits that are "chewed" by cardinals. If the cardinal flies away with the fruit, even without swallowing the seeds, it may still deliver short distance dispersal. Nonetheless, it appears that mammals may be the primary dispersal agents for these large fruits.

The presence of a red preripec fruit color is also characteristic of summer mammal-bird fruits. The bi-color display of unripe red and ripe blue-black fruit may increase the conspicuousness of the fruiting display (Thompson and Willson 1979, Stiles 1980, 1982, Stapanian 1982, White and Stiles unpub. ms.). All seven of the hammock mammal-bird fruit species show a red preripec fruit color compared to

only 2 of the 11 fall fruiting species and 2 of the 19 fall-winter fruiting species.

Fall Fruiting

The 11 fall fruiting species in the hammock community include 5 species, Cornus foemina, Cornus florida, Euonymus americanus, Parthenocissus quinquefolia, and Magnolia grandiflora, with high lipid content ($> 10\%$ dry mass, Appendix III). High lipid content has typically been correlated with high fruit quality as lipids yield about twice the energy content as carbohydrates (Stiles 1980, Herrera 1982a). As a group, fall fruiting species show the highest mean percentage in lipid content compared to the other fruiting patterns (Table 3-1). These high-lipid fruits become available in the early fall, when local frugivore diversity and abundance are at a peak due to the presence of migrant frugivores. Herrera (1982a, 1984a) has also found a strong correlation between the timing of production of lipid-rich fruits by bird-dispersed plants in the fall and frugivore abundance in the scrublands of southern Spain.

High quality fruits, because of their high lipid content, may also attract insects and microbes. This may result in more rapid spoilage of high-lipid fruits compared to low-lipid fruits (Janzen 1977, Stiles 1980) and thus emphasize the importance of high fruit removal rates. All

five fall high-lipid fruits showed some fruit damage resulting from invertebrate and microbe attack.

According to White and Stiles (unpub. ms.), production of lipid-rich fruits in eastern North America may be limited by season and plant growth form. These fruits tend to be produced in the fall when flocks of vagile, hyperphagic migrant frugivores are available for rapid fruit removal, and appear also to be limited to woody shrubs and trees, which can produce moderate to large fruit crops. The small fruit crops of herbs may limit repeat visits by birds and thus decrease selection for high-lipid fruits (Stiles and Devito, unpub. ms.). Based on the analysis of 77 species of mid-latitude bird-dispersed fruits from eastern North America, White and Stiles (unpub. ms.) have found that fruits with lipid contents greater than 10% are limited to fall fruiting woody plants. A similar situation occurs for the lower latitude hammock community. No summer fruiting species produces a high-lipid fruit, while 5 of the 11 fall fruiting species show fruits rich in lipids. High lipid fruits are also found among fall-winter fruiting species (see below). High lipid fruits in the hammock community are limited to woody plants, no herbaceous plants produced high lipid fruits (see below).

Stiles (1980) has proposed two dispersal strategies for fall fruiting plants involving high quality fruits (above) and low quality fruits (< 10% dry lipid mass). Low quality fruits may be less attractive to birds, but also less prone

to decay, thus permitting slower removal rates. Based on Stiles' dichotomy, Callicarpa americana, Crataegus uniflora, Aralia spinosa, Arisaema dracontium, Phytolacca americana, and Amelopsis arborea would be considered low quality fruits in the hammock community. With the exception of Arisaema dracontium and Crataegus uniflora, these species produce low lipid fruits (< 3.0% dry mass) with small seed masses (mean = 9.2mg) and low seed loads (mean = 16.6%).

Crataegus uniflora fruits show characteristics of mammal-bird fruits (low persistence, sweet taste, large fruit mass) and appear to be adapted primarily for mammal dispersal. The herb Arisaema dracontium produces low-reward fruits for birds due to their high seed load (40.4%), low lipid content (2.1%), and low yield in dry matter per fruit (31.3mg). Stiles and Devito (unpub. ms.) have suggested that certain low quality, rare herbs may rely on generalized mimicry of high-quality fruits for seed dispersal. Arisaema dracontium fruits resemble fallen Cornus florida fruits (a high-lipid fruit) and may be taken accidentally by ground foraging thrushes and robins.

Fall-Winter Fruiting

Fall-winter fruiting species (19 species) produce highly persistent fruits that are available to migrant frugivores in the early fall and to overwintering frugivores throughout the winter and early spring. Fall-winter fruits

show the lowest mean fruit mass (251.8mg) and lowest mean water content (55.4%) of the four seasonal fruiting patterns (Table 3-1). The low water content of these fruits may be an adaptation for persistence (Stapanian 1982, White and Stiles unpub. ms.). Contrastingly, summer fruits show a high mean water content (82.7%) and are poorly persistent.

Fall-winter fruiting species include 5 species, Persea borbonia, Symplocos tinctoria, Myrica cerifera, Rhus coppalina and Toxicodendron radicans, that show high lipid content. White and Stiles (unpub. ms.) have recognized three distinct fruit types for lipid-rich fruits: 1) waxy-pulped fruits, 2) dry (< 30% water), oily fruits of the genus Rhus, and 3) moist (> 40% water), fleshy fruits of the high-quality fruiting pattern. Toxicodendron radicans and Myrica cerifera would be considered waxy-pulped fruits and will be discussed below. Rhus coppalina (12.0% lipid) would be considered a dry, oily, lipid-rich fruit. The fruits of Rhus, although fed on by six bird species (Appendix IV), were taken infrequently. Over a two-year period, I observed only 12 visits to this species, in which 190 fruits were removed. Sumacs (Rhus spp.) generally are considered to be unattractive to birds and are used primarily as an emergency food source (White and Stiles, unpub. ms.).

Persea borbonia and Symplocos tinctoria would be considered fleshy, high-quality, lipid-rich fruits. Symplocos tinctoria also had the highest protein content (13.3%) of the 43 species analyzed. The long fruiting

duration for these species is unusual for lipid-rich fruits of North America. Symplocos had a highly asynchronous fruit ripening pattern (Chapter II), resulting in a small standing crop of ripe fruits at any one time. This resulted in high removal rates of ripe fruits (see below), thus limiting the number of ripe fruits available for insects and microbes. The fruits of Symplocos also turned from purple and moist to brown and dry. Persea borbonia fruits showed little evidence of extensive damage from insects or microbes. This species may possess effective toxins that discourage insect and microbe attack.

Winter Fruits

The 4 winter fruiting species produced ripe fruits in January when the majority of fall-fruiting species showed depleted fruit crops. The fruits of Prunus caroliniana, Osmanthus americanus, and Ilex opaca showed a nutrient content similar to that of fall-winter low-quality fruits (lipid content < 2.5%), while Phoradendron serotinum exhibited a distinct fruit type and dispersal syndrome from the other fall-winter and winter fruiting species (see below). Prunus caroliniana, Osmanthus americana, and Ilex opaca produced large fruits (mean fruit mass = 552.4mg), suggesting that they may be adapted primarily for dispersal by robins, the most abundant frugivore at this time.

Specialized Dispersal Systems

Several specialized dispersal systems, involving single plant species that are dependent upon a small set of dispersal agents, occur in the hammock community. Such associations are rare in bird-fruit dispersal systems (Wheelwright and Orians 1982) and typically involve fruits with distinct fruit structure or chemistry (White and Stiles unpub. ms.). Toxicodendron radicans and Myrica cerifera produce waxy-pulped fruits unlike the fleshy-pulped fruits exhibited by most species in the hammock. These species produce high lipid fruits, which may be a necessity for plants that have a small dispersal coterie (McKey 1975). Removal of Toxicodendron fruits in the hammock is limited to woodpeckers and Yellow-rumped Warblers (Dendroica coronata) (Appendix IV). Based on gut content records of fruit-eating birds in North America, White and Stiles (unpub. ms.) have found woodpeckers and warblers to use waxy-pulped fruits significantly more frequently than other fruit-eating birds. Greenberg (1984) also found a close relationship between warblers and the waxy fruits of Lindakeria laurina in Panama. Removal of Myrica cerifera fruits in the hammock is limited primarily to Yellow-rumped Warblers. These warblers accounted for 91% of the total visits to M. cerifera.

A similar situation exists between the hemiparasite Phoradendron serotinum and the Cedar Waxwing (Bombycilla

cedrorum). Cedar Waxwings accounted for 80.7% of the total visits to Phoradendron; mistletoe constituted 70.5% of the total visits to fruiting plants by waxwings. Mistletoe fruits show a distinct fruit structure typical of many mistletoe species (Gill and Hawksworth 1961), while waxwings probably show similar morphological fruit-eating adaptations to those of other mistletoe birds (Wetmore 1914, Walsberg 1975). Phoradendron berries also have a high protein content (11.5%), which may contribute to its prevalence in the waxwing's diet.

Fruit Removal

The high lipid fruiting species, Cornus foemina and Symplocos tinctoria, had consistently high fruit removal rates. Removal rates for Cornus foemina, a fall fruiting species, increased in early September upon the arrival of migrant frugivores (Fig. 3-1). Fruit removal remained high throughout September until its fruit crops were exhausted in late September. Symplocos tinctoria, a fall-winter fruiting species, had high weekly removal rates from August through January (Fig. 3-2). This species exhibited a highly asynchronous ripening pattern (Chapter II). This resulted in a relatively small standing crop of ripe fruits that was visited regularly by a number of birds (Appendix IV).

The fall fruiting Aralia spinosa, a low lipid fruit, showed high removal rates in 1983 and 1984 (Fig. 3-1). This

Fig. 3-1. Fall fruiting species. Percent of the initial total number of fruits removed within a single week for Cornus foemina, Callicarpa americana, and Aralia spinosa. Solid line represents 1982 season, dashed line 1983 season.

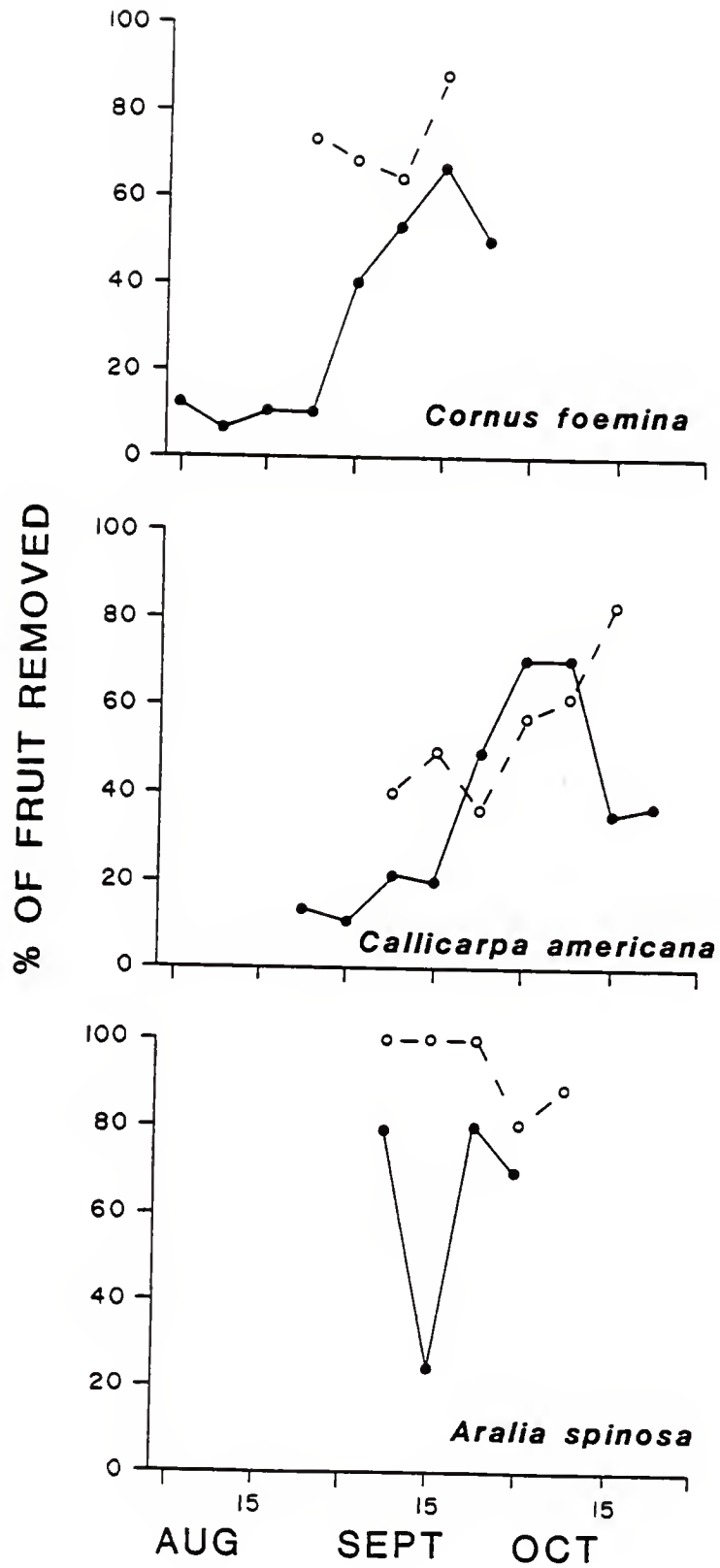
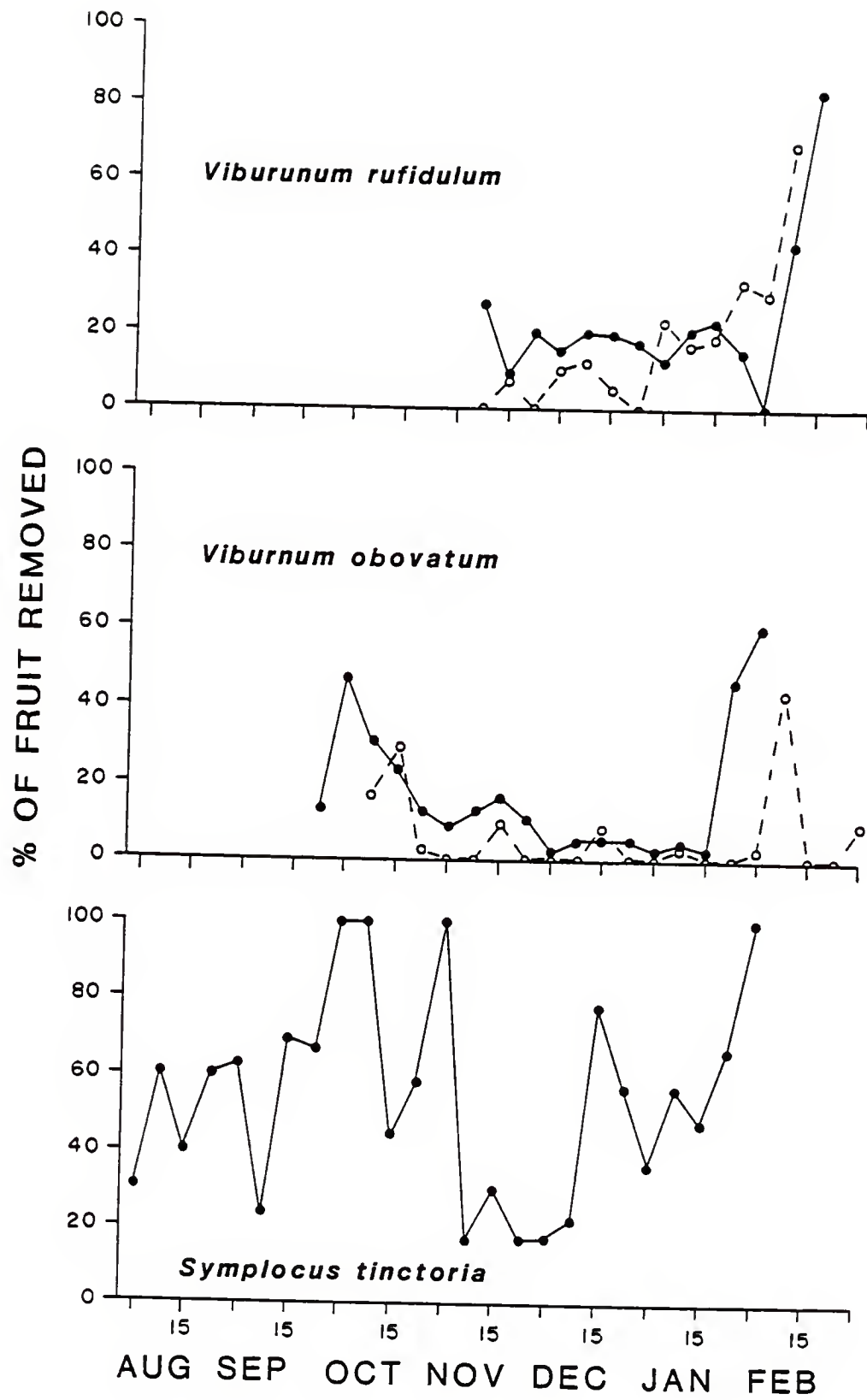
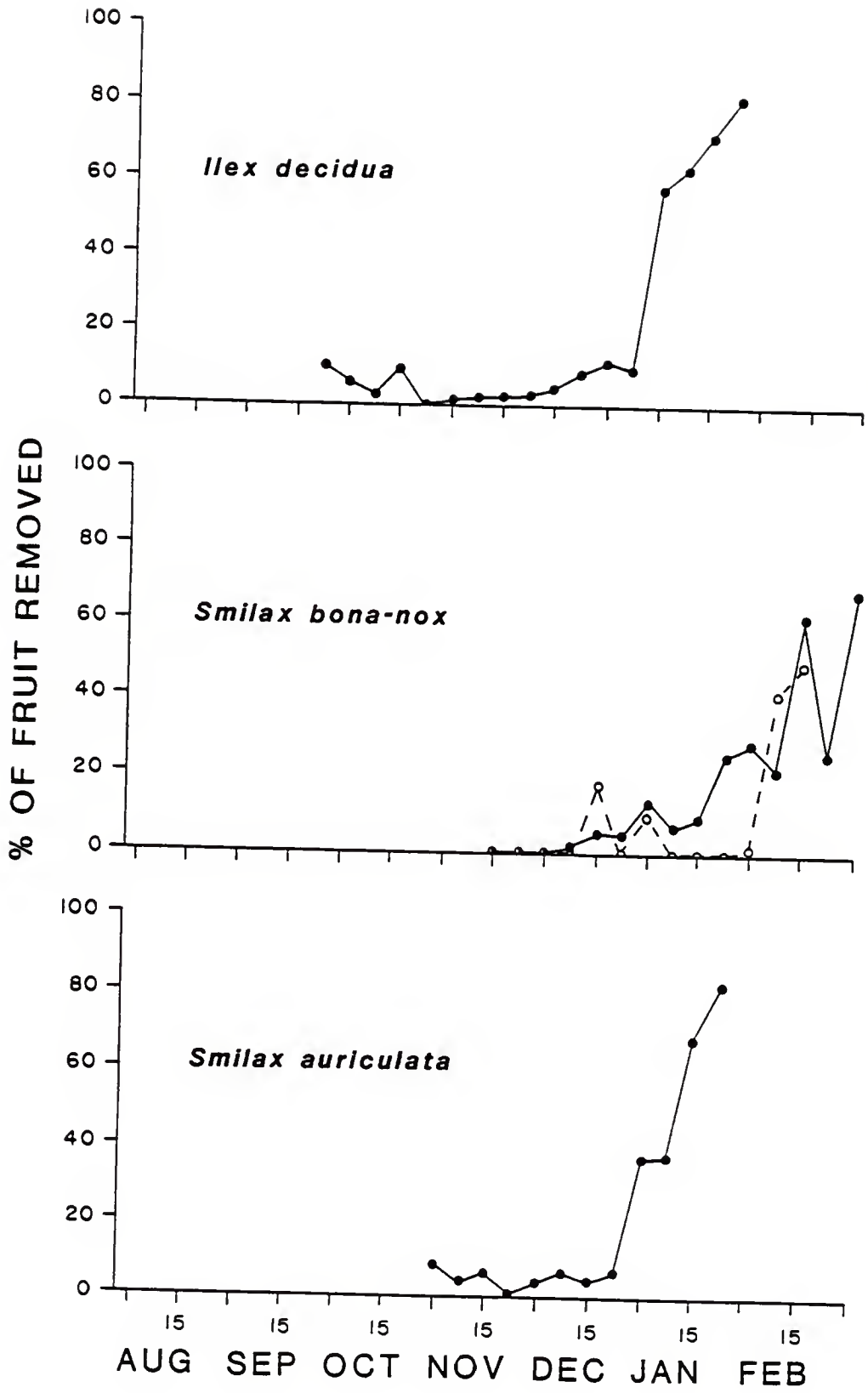


Fig. 3-2. Fall-winter fruiting species. Percent of the initial total number of fruits removed within a single week for Viburnum rufidulum, Viburnum obovatum, Symplocos tinctoria, Ilex decidua, Smilax bona-nox, and Smilax auriculata. Solid line represents 1982-83 season, dashed line 1983-84 season.





plant was visited regularly by small flocks of migrant thrushes (Appendix IV) and was considered a primary plant species for the local frugivores. The showy fruiting display, abundant fruit crop, clumped distribution, and low seed load of its fruits (14.9%), may account for the attractiveness of this species to fruit-eating birds. High removal rates appear to be advantageous for Aralia as its fruits are highly susceptible to drying out and rotting.

Callicarpa americana, another fall, low lipid fruiting species, showed a fruit removal pattern similar to Aralia's. Removal rates for Callicarpa were high in September and October until its fruit crops were exhausted (Fig. 3-1). This species, which was visited regularly by migrant thrushes (Appendix IV), has a stunning fruiting display and was highly visible in the hammock. The popularity of Callicarpa may also be attributed to its individual abundance, large fruit crops, and the low seed load of its fruits (11.1%).

Fall-winter low lipid fruits typically showed low removal rates throughout the fall until January or February, when removal rates increased. These increases occurred after the fruit crops of the fall and fall-winter high lipid fruiting species were all removed. This pattern is shown by Ilex decidua, Smilax bona-nox, Smilax auriculata, Viburnum obovatum, and Viburnum rufidulum (Fig. 3-2). Often the increase in removal rates was dramatic for these low-quality fruits. Sharp increases in removal rates were typically the

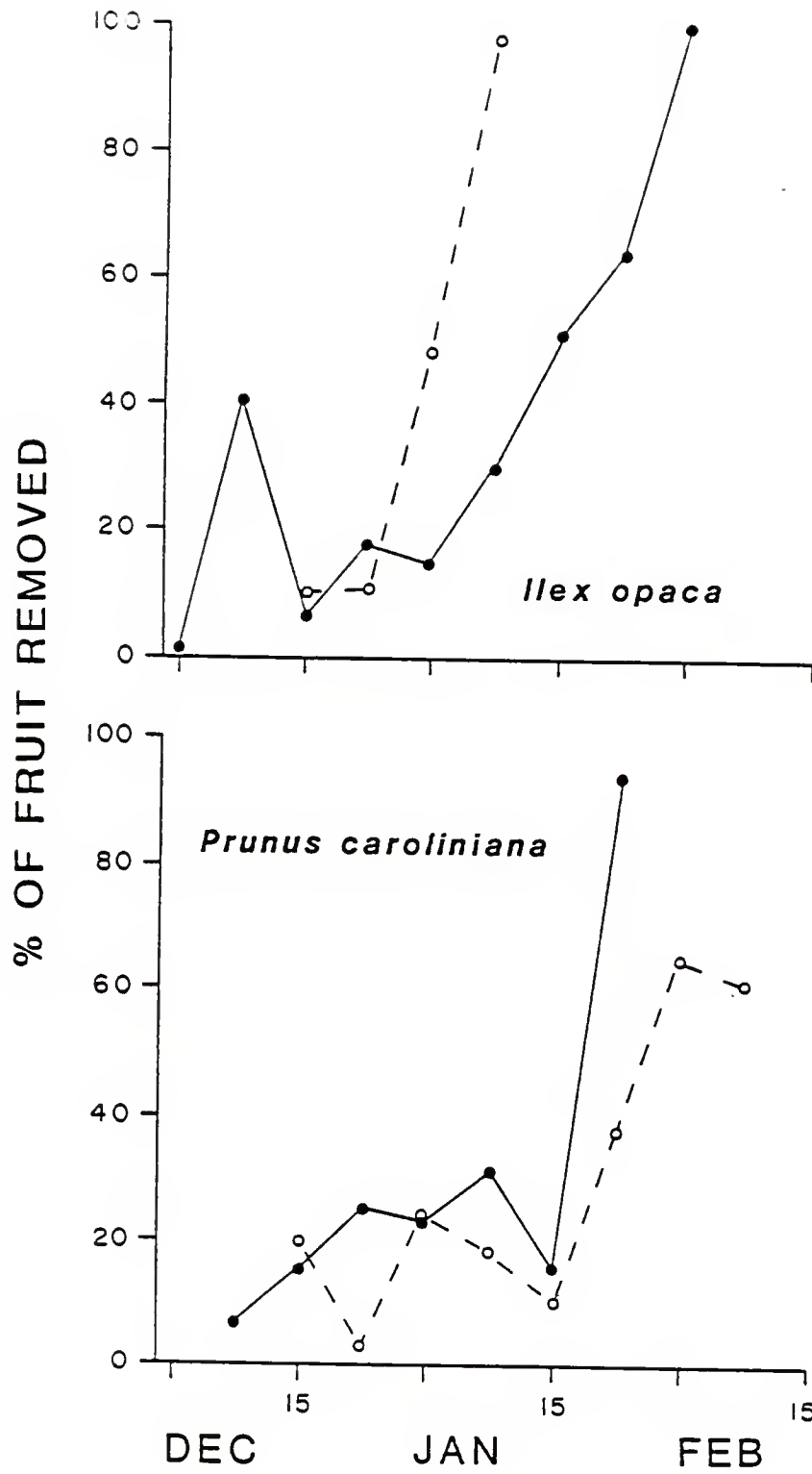
result of the inclusion of a specific fruit in the diet of robins, the most abundant wintering frugivore in the community. Once a fruit was included in the robin's diet, its fruit crop was regularly visited until it was exhausted.

The winter fruiting Prunus caroliniana showed a fruit removal pattern similar to those of fall-winter low quality fruits. Removal rates of Prunus were moderate until it became the primary fruit for robins. At this time, the removal rates for this species increased sharply until its fruit crop was completely removed (Fig. 3-3). The attractiveness of Prunus caroliniana to robins may be due to several factors. Its fruits, while having a low lipid content and high seed mass, have three times the dry pulp mass of fruits of its congener, P. serotina, a summer fruiting species. Also, the large seed of Prunus caroliniana is regurgitated, which may negate the disadvantages of a high seed load (Sorensen 1984).

Seasonal Patterns of Fruit Removal

Based on weekly observations of fruit-eating birds from 1982-84 and fruit removal rates of marked individuals, the fruit removal picture in the hammock community appears as follows. In the early fall, when frugivore availability is high due to the presence of migrant frugivores, high lipid and some low lipid fruits are removed at a rapid rate. These low lipid fruits exhibit a low seed load and offer transient frugivores an abundant, highly visible food

Fig. 3-3. Winter fruiting species. Percent of the initial total of fruits removed within a single week for Ilex opaca and Prunus caroliniana. Solid line represents 1982-83 season, dashed line 1983-84 season.



source. Fall high lipid fruiting species often had small fruit crops (e.g. Symplocos tinctoria, Magnolia grandiflora) or may be more difficult to locate (e.g. Parthenocissus quinquefolia) than many low lipid species. Thus, while lipid-rich fruits may offer a higher caloric reward to birds, the search time for these fruits may be higher than for some low-quality species. Therefore it may be practical, energetically, for a transient frugivore to visit abundant low lipid fruits (e.g. Aralia, Callicarpa) when lipid-rich fruits are not readily visible.

Cornus florida, with its lipid-rich fruit, is the primary fruiting plant in the mid-fall, when it is visited by small flocks of migrant thrushes and later, robins (Appendix IV). In late fall, when the fruit crop of Cornus florida is completely removed, Persea borbonia, another high lipid species, becomes the primary fruit for wintering frugivores. The size of the fruit crop of Cornus florida and Persea borbonia varies greatly in different years and the size of their crops appears to influence frugivore numbers in the hammock.

Nonetheless, while Cornus florida and Persea borbonia were primary food plants for local frugivores during late fall and early winter, other fruiting species were also visited daily. On one day in mid-November, I observed robins feeding on the fruits of 4 species, including 2 low-quality species, despite the presence of large Cornus florida fruit crops. Feeding on a diversity of fruits

appears to be a common practice among many frugivorous birds (Snow 1977, Wheelwright 1983, Herrera 1984a) and may be related to dietary requirements or "optimal foraging". The varied feeding behavior of frugivorous birds may be essential to low-reward or rare species that by themselves would be unable to attract dispersers. Therefore, at the community level, there is an interdependence, in relation to dispersal, in which low-reward species may benefit from coexisting with primary plant species (Herrera 1984a).

In late January, when the fruit crop of Persea borbonia is gone, the hammock frugivores shift to persistent, low lipid fruits such as Prunus caroliniana, Osmanthus americanus, Celtis laevigata, Ilex spp., and Vaccinium arboreum. The last fruits to be taken include low lipid Smilax spp., Mitchella repens, and Viburnum obovatum. At this time wintering frugivores are beginning to lay down fat deposits for the northward migration to their breeding grounds.

I found no absolute relationship between high and low-quality fruits and fruit removal rates. The majority of high-quality fruits did show higher fruit removal rates than most low-quality species, however, certain low-quality species (e.g. Callicarpa americanus, Aralia spinosa) exhibited fruit removal rates comparable to high-quality species and were considered primary plants in the community. Herrera (1984a) also found no consistent relationship between fruit quality and removal success. Thus other

factors, including crop size, fruiting display, seed load, and plant distribution, may be equally as important as lipid content in relation to removal success. This suggests that the dichotomy of high and low-quality fruits, as based on lipid content (McKey 1975, Howe and Estabrook 1977), may not always be correlated with fruit removal success.

Eastern North American Comparisons

The bird-dispersed flora of San Felasco Hammock shows a close taxonomic affinity to the mid-latitude flora of eastern North America. This is especially evident at the generic level: 23 of the 31 genera present in the hammock are found at mid-latitudes. White and Stiles (unpub. ms.) have analyzed the nutritional content of 77 species of mid-latitude bird-dispersed plants of eastern North America. At the generic level, 22 Florida species in 13 genera showed similar nutritional composition to 33 congeners from New Jersey. Of 7 species common to San Felasco Hammock and New Jersey, 3 had marked nutritional differences. Parthenocissus quinquefolia fruits collected in New Jersey were found to have a lower lipid content than fruits from Florida (16.2% vrs. 35.9%). Stapanian (1982) also found higher lipid values for Parthenocissus fruits in Kansas than in New Jersey (21.8% vrs. 16.2%). Euonymus americanus fruits from Florida were also richer in lipids than fruits from New Jersey (38.2% vrs. 7.0%). A high lipid

content for the congener, E. atropurpureus (31.2%) has also been recorded (Johnson et. al. 1985). Finally, Nyssa sylvatica, a high-quality fruit as determined by White and Stiles, showed a much lower lipid content in Florida than in New Jersey (1.4% vrs. 14.8%).

The bird-dispersed flora of San Felasco hammock has a high proportion of lipid-rich fruits compared to floras of more northern latitudes. This is due in part to the inclusion of such tropical-affiliated species as Magnolia grandiflora, Persea borbonia, and Symplocos tinctoria. These species occur in families that have characteristically high lipid fruits (e.g. Lauraceae). The mild Florida winters have permitted the establishment of these subtropical species and have also resulted in large populations of wintering frugivores. Furthermore, a number of these species show extended fall-winter fruiting, using wintering frugivores for seed dispersal. At more northern latitudes, small populations of wintering birds should select against the evolution of lipid-rich fall-winter fruits. Thus, high lipid fruits are limited to fall fruiting species at middle and upper temperate latitudes (Thompson and Willson 1979, White and Stiles unpub. ms.).

The remaining high lipid fruits from the hammock community belong to species from temperate families (e.g. Cornaceae) or families with wide geographic distribution (e.g. Vitaceae). These families typically show some variability in the lipid content of their fruits. For

example, the Vitaceae shows both high and low lipid fruiting species in the hammock. The fall fruiting Parthenocissus quinquefolia has a high lipid fruit, while the summer fruiting Vitis rotundifolia and V. aestivalis have low lipid fruits. The variability in fruit quality in temperate families suggests an independent evolution of lipid-rich fruits for these families (White and Stiles, unpub. ms.).

Conclusions

The 43 species of bird-dispersed plants in the hammock community represent a heterogeneous mixture of fruit types, which exhibit a wide range in nutrient composition. Nonetheless, clear nutritional patterns related to dispersal strategies and seasonality are evident. Grouping species into categories is thus possible. Summer fruiting species form a distinct set, in which fruit morphology and nutrient composition show characteristics (e.g. sweet taste, low persistence) that may favor mixed mammal-bird seed dispersal. This strategy appears to be an adaptation to the low abundance of frugivores during the summer months and to the preference of breeding birds for insects as their primary food supply.

Fall fruiting species fall into two categories, high lipid and low lipid fruiting species. High lipid fruits present migrant birds with an energy-rich food source and consequently show high rates of fruit removal. Low lipid

fruits, while designated as low-quality, may offer migrants an abundance of fruits with low seed loads. Low lipid fruiting species show variable removal rates, with some species showing low removal rates, while others exhibit removal rates comparable to high lipid species.

Fall-winter fruiting species also consist of high and low lipid species, in which the high lipid species typically have their fruit crops removed before the low lipid species. Low lipid fruits persist until late winter - early spring, when they are taken sequentially by flocks of robins.

Winter fruiting species have fruits with low lipid content and exhibit fruit removal patterns similar to low lipid fall-winter fruiting species. The delayed ripening pattern of these species may be an adaptation for the avoidance of competition for dispersal agents from high lipid species.

Within the hammock community are a series of primary fruiting plants. These plants receive the majority of visits from local frugivores and may be instrumental in attracting flocks of migrant frugivores into the community. Less preferred fruiting species may thus benefit from coexistence with these primary plant species. Primary plant species included both high and low lipid species. Characteristics of primary plants that may account for their popularity include high lipid content, large fruit crops, clumped distribution, and low seed loads.

The nutritional patterns of bird-dispersed fruits in northern Florida show strong similarities to those patterns described by Stiles (1980) and White and Stiles (unpub. ms.) for mid-latitude bird-dispersed plants of eastern North America. These similarities are the result of the close taxonomic relationship in the bird-dispersed floras of the two regions and to similar selection pressures related to the seasonal availability of frugivores. The major difference in the bird-fruit system between middle and lower temperate latitudes in eastern North America is the prevalence of the fall-winter fruiting pattern at lower latitudes compared to middle latitudes. Mild southern winters have permitted the establishment of high lipid, bird-dispersed species of tropical affinity and large populations of wintering frugivores at lower latitudes, which have selected for fall-winter fruiting for many species. The presence of these subtropical species has resulted in a greater proportion of high lipid fruits in the bird-dispersed flora at lower latitudes compared to middle and upper latitudes in eastern North America.

CHAPTER FOUR SUMMARY

The bird-fruit dispersal system of San Felasco Hammock involves 22 species of frugivorous birds and 45 species of bird-dispersed plants. The frugivorous birds include members from eight families and range in size from approximately 5 to 400g. Twelve of the twenty-two bird species are considered major frugivores as they were involved in the majority of fruit visitations. The bird-dispersed flora consists of plants representing 23 families. These plants show high variability in fruit type and composition.

The fruiting phenology of the bird-dispersed plants of San Felasco Hammock show similarities to both tropical and middle latitude temperate bird-dispersed plant fruiting systems. The hammock community shows ripe fruit every month of the year, as is typical of many tropical communities (Daubenmire 1972, Frankie et. al. 1974, Putz 1979, Liebermann 1982, Wheelwright, in press). Bird-dispersed plants of middle temperate latitudes tend to fruit only during the summer and fall, few species bearing ripe fruit during the winter months (Thompson and Willson 1979). The timing of fruit ripening in the hammock community, however, is highly seasonal and appears to be strongly influenced by the availability of migrant frugivores. This is a similar

situation to that observed at middle temperate latitudes in North America (Thompson and Willson 1979, Stiles 1980, White and Stiles unpub. ms.).

Most bird-dispersed plants in the hammock bear ripe fruit in the fall, when the community is invaded by a high diversity of migrant frugivores. Frugivore diversity and abundance remain high throughout the fall and winter months as does the number of fruiting species. The number of fruiting species decreases in the spring and remains low throughout the summer months. Frugivore diversity and abundance is also low at this time.

The 44 species of bird-dispersed plants fall into four distinct seasonal fruiting patterns: summer fruiting, fall fruiting, fall-winter fruiting, and winter fruiting. Most summer fruiting species have fruit characterized by high water content, large fruit mass, high carbohydrate content, sweet taste, and low persistence. These species produce "mammal-bird" fruits that may depend on mammals and birds for dispersal. Summer fruiting species typically are rare or uncommon in the community and occur in disturbed habitats.

Fall fruiting species produce ripe fruits during the peak of fall migration of frugivorous birds through northern Florida. Fall fruiting species include five species that show high lipid ($> 10\%$ dry mass) content and are thus considered high-quality fruits. Fall species also include low lipid (low-quality) fruiting species that produce fruits

with low seed loads. Fall fruiting species usually occur in the closed forest and are common or abundant in the community.

The fall-winter fruiting pattern is the most prevalent fruiting pattern in the hammock, being shown by 20 species. Fall-winter fruiting species produce highly persistent fruit that become ripe in the fall, persisting into January and February. This fruiting pattern is thus synchronized with the first wave of transient frugivores and also the second wave of overwintering frugivores. Fall-winter fruiting species are typically evergreen, and their fruits have the lowest mean fruit mass and water content of the four fruiting patterns. Six fall-winter fruiting species have high lipid fruits, including two with waxy-pulped fruit, one with dry fruits, and three with moist fleshy fruits. The remaining fall-winter fruits produce low lipid fruits.

The winter fruiting pattern is shown by 4 evergreen species, in which fruit maturation does not occur until December. These species use only overwintering frugivores for seed dispersal. Winter fruiting species exhibit low lipid fruits, although Phoradendron serotinum produces a relatively high protein fruit and a unique dispersal syndrome compared to the other winter species.

The bird-fruit dispersal system of the hammock community is characterized by a sequence of primary plant-bird interactions. Primary plant species receive the majority of visits from fruit-eating birds and may be

instrumental in attracting frugivorous birds into the community. These primary plants may also indirectly favor seed dispersal of non-primary plants due to the varied diets exhibited by fruit-eating birds. The primary plants in this community consist primarily of high lipid fruiting species (e.g. Parthenocissus quinquefolia, Cornus florida, Persea borbonia), but also include several low lipid fruiting species (e.g. Aralia spinosa, Callicarpa americana). These low lipid species produce large fruit crops and high carbohydrate fruits with small seeds and low seed loads. Primary plants show high removal rates, whereas fall-winter low quality fruiting species exhibit low removal rates until January or February when the fruit crops of Cornus florida and Persea borbonia are exhausted. At this time, the fruits of these highly persistent species are taken regularly until their fruit crops are gone.

Primary frugivore bird species in the hammock include migrant thrushes in the early fall and robins in the late fall and winter. Transient Veerys are the primary dispersal agent in the early fall when they form small flocks and visit a variety of fruiting species. When Veerys leave the hammock in the late fall, robins, due to their large numbers and highly frugivorous diet become the primary dispersal agent in the community. Robins become the primary disperser for a sequence of fruiting plants, including Cornus florida, Persea borbonia, and Prunus caroliniana. Robins are also

responsible for the bulk of the fruit removal of the fall-winter low quality fruiting species in January and February.

Several specialized dispersal systems, involving single plant species that are dependent upon a single or few dispersal agents, are evident in the hammock community. These include a close relationship between the mistletoe, Phoradendron serotinum and the Cedar Waxwing, Toxicodendron radicans and woodpeckers and Yellow-rumped Warblers, and Myrica cerifera and the Yellow-rumped Warbler. These plant species produce fruits with a distinct fruit structure or chemistry related to their dispersal syndromes.

The bird-dispersed plants of the lower temperate latitude hammock community show similar phenological patterns and fruit characteristics to middle latitude temperate bird-dispersed plants of North America. Fall fruiting is the most prevalent fruiting pattern shown at middle latitudes of North America, where the timing of fruiting is closely correlated with the availability of migrant frugivores (Thompson and Willson 1979). At lower latitudes, the fall fruiting pattern is also common; however, the fall-winter fruiting pattern is shown by the largest number of species. Thus while 26 species of bird-dispersed plants have ripe fruit during the winter months in the hammock community, only 4 species in Illinois have fruit at this time. High frugivore availability, mild winters, and the presence of evergreen species have made winter

fruiting possible and profitable in northern Florida compared to the middle latitudes of North America.

Similar selection pressures related to frugivore availability and close taxonomic affinities have resulted in close similarities in the fruit characteristics of the bird-dispersed flora between lower and middle temperate latitudes of eastern North America. Nonetheless, the bird-dispersed flora of the hammock community shows a higher proportion of lipid-rich fruits than at more northern latitudes. This is due in part to the inclusion within its flora of such lipid-rich tropical-affiliated species as Magnolia grandiflora, Persea borbonia, and Symplocos tinctoria.

The bird-dispersed flora of the hammock community also shows fruiting patterns and fruit characteristics similar to the lower temperate latitude scrubland community of southern Spain (Herrera 1981, 1982a, 1984a). Both communities show a predominance of fall-winter fruiting species, in which lipid-rich fruits are produced in the fall. This pattern can be attributed to similar patterns of frugivore availability, in which the presence of overwintering frugivores in both communities has selected for fall-winter fruiting and also to the high degree of evergreenness characteristic of both communities.

APPENDIX I. METHODS OF CALCULATING RIPENING
SYNCHRONY (MODIFIED FROM AUGSPURGER 1983)

- A. Synchrony of a given individual with its conspecifics: X_i , the index of synchrony for individual i , is defined as:

$$X_i = \left(\frac{1}{n-1} \right) \left(\frac{1}{f_i} \right) \sum_{j=1}^n e_j \neq 1$$

where, e_j = number of days both individuals i and j are ripening 90% of fruit crop, $j \neq i$; f_i = number of days individual i is ripening 90% of fruit crop; n = number of individuals in population.

When $X = 1.0$, perfect synchrony occurs, i.e., ripening period of individual i overlaps with ripening period of each other individual, $j \neq i$ in the population.

When $X = 0.0$, no synchrony occurs, i.e., no overlap occurs in the ripening period of individual i and any other individual, $j \neq i$ in the population.

- B. Synchrony of the population:
 Z , the index of population synchrony, is defined as:

$$Z = \frac{1}{n} \sum_{i=1}^n X_i$$

where X_i is synchrony of individual i with its conspecifics from part A. (above).

APPENDIX II. FLOWERING AND FRUITING SCHEDULES OF
BIRD-DISPERSED PLANTS OF SAN FELASCO HAMMOCK, FLORIDA

Family Species	1982-83		1983-84		Fruiting Period	Flowering Period	Fruiting Period	Fruiting Pattern (Abundance)*
	Flowering Period	Fruiting Period	Flowering Period	Fruiting Period				
Anacardiaceae								
<u>Toxicodendron radicans</u>	apr-may	sep-jan	apr-may	oct-jan	F-W (A)			
<u>Rhus copallina</u>	jul-aug	sep-apr	aug	aug-apr	F-W (C)			
Aquifoliaceae								
<u>Ilex glabra</u>	may-jun	oct-mar	may	nov-apr	F-W (U)			
<u>Ilex opaca</u>	apr-may	nov-mar	may-jun	dec-feb	W (A)			
<u>Ilex decidua</u>	apr-may	sep-mar	mar-apr	oct-feb	F-W (C)			
<u>Ilex cassine</u>	may	oct-mar	may	oct-feb	F-W (A)			
Araceae								
<u>Arisaema dracontium</u>	-	-	mar-apr	oct-dec	F (R)			
Araliaceae								
<u>Aralia spinosa</u>	jul	aug-oct	aug	aug-oct	F (A)			
Caprifoliaceae								
<u>Viburnum obovatum</u>	feb-mar	sep-mar	mar-apr	oct-apr	F-W (U)			
<u>Viburnum rufidulum</u>	mar-apr	oct-mar	mar-may	oct-mar	F-W (A)			
Celastraceae								
<u>Eunonymus americanus</u>	may-jun	sep-dec	may-jun	sep-feb	F (C)			
Cornaceae								
<u>Cornus florida</u>	feb-mar	sep-dec	mar-apr	sep-dec	F (A)			
<u>Cornus foemina</u>	apr-may	jul-sep	may-jun	aug-oct	F (A)			
<u>Nyssa sylvatica</u>	apr-may	nov-feb	may	oct-jan	F-W (C)			
Ericaceae								
<u>Vaccinium arboreum</u>	mar-apr	sep-mar	apr-jun	oct-mar	F-W (A)			
<u>Vaccinium myrsinites</u>	feb-mar	apr-jun	feb-mar	apr-jul	S (U)			

APPENDIX III. FRUIT TRAITS ANALYZED FOR BIRD-DISPERSED
PLANTS OF SAN FELASCO HAMMOCK, FLORIDA. FRUITING PATTERNS:
S=SUMMER, F=FALL, F-W=FALL-WINTER, W=WINTER

FAMILY Species (Code)	Fruit Mass (mg)	Seed Mass (mg)	Seed Load (%)	Dry Pulp (mg)	Water (%)	Lipid (%)	Pro (%)	Cho (%)	Fruiting Pattern
ANACARDIACEAE									
<u>Rhus coppalina</u> (RC)	7.6	3.5	46.8	3.6	10.1	12.0	5.4	4.5	F-W
<u>Toxicodendron radicans</u> (TR)	21.9	14.9	68.0	5.2	3.6	47.2	2.0	0.0	F-W
AQUIFOLIACEAE									
<u>Ilex cassine</u> (IC)	96.2	7.9	32.9	18.2	71.8	0.9	3.1	32.8	F-W
<u>Ilex decidua</u> (ID)	188.9	16.3	34.6	40.3	67.4	1.3	3.8	29.1	F-W
<u>Ilex glabra</u> *(IG)	181.4	3.4	10.5	51.0	68.6	0.7	1.9	52.0	F-W
<u>Ilex opaca</u> (IO)	400.8	23.3	23.3	130.4	57.6	0.2	2.8	39.9	W
ARACEAE									
<u>Arisaema dracontium</u> (AD)	242.0	97.8	40.4	31.3	78.3	2.1	2.1	77.6	F
ARALIACEAE									
<u>Aralia spinosa</u> (AS)	118.4	3.5	14.9	13.4	86.7	2.4	3.0	47.5	F
CAPRIFOLIACEAE									
<u>Viburnum obovatum</u> (VO)	117.8	55.2	46.8	31.6	49.5	5.8	1.8	49.6	F-W
<u>Viburnum rufidulum</u> (VR)	384.1	104.1	27.1	125.7	55.1	5.2	1.2	61.6	F-W
CELASTRACEAE									
<u>Euonymus americanus</u> (EA)	215.9	34.2	50.6	28.6	73.2	38.2	5.0	17.3	F
CORNACEAE									
<u>Cornus florida</u> (CF)	131.3	32.1	24.4	34.8	64.9	33.5	2.7	24.8	F
<u>Cornus foemina</u> (CFO)	326.6	91.3	27.9	84.7	64.0	27.1	2.8	23.4	F
<u>Nyssa sylvatica</u> (NS)	716.0	206.3	28.8	118.8	76.7	1.4	4.7	50.5	F-W
ERICACEAE									
<u>Vaccinium arboreum</u> (VA)	208.8	0.6	32.6	46.1	67.2	1.1	3.0	51.0	F-W
<u>Vaccinium myrsinites</u> (VM)	184.2	0.7	13.0	21.6	86.5	2.5	2.4	42.3	S
LAURACEAE									
<u>Persea borbonia</u> (PB)	1044.5	800.5	76.6	123.9	49.2	40.5	5.4	11.5	F-W
LILIACEAE									
<u>Smilax auriculata</u> (SMA)	258.9	34.8	33.6	37.7	78.1	0.9	3.5	50.9	F-W
<u>Smilax bona-nox</u> (SMB)	165.2	74.5	45.1	26.5	70.8	0.6	6.6	25.5	F-W
<u>Smilax pumila</u> (SMP)	173.2	50.9	29.4	30.7	74.9	1.9	4.9	48.6	F-W

<u>Smilax smallii</u> (SMS)	228.4	28.1	25.8	55.9	67.1	1.8	6.7	42.5	S
<u>Smilax tamnoides</u> (SMT)	256.6	80.8	44.1	42.8	70.2	1.4	6.6	55.8	F-W
MAGNOLIACEAE									
<u>Magnolia grandiflora</u> (MG)	249.0	88.7	35.7	106.7	33.4	61.0	4.0	20.1	F
MORACEAE									
<u>Morus rubra</u> *(MRU)	780.1	1.6	3.9	81.9	85.6	1.1	5.9	66.4	S
MYRICACEAE									
<u>Myrica cerifera</u> (MC)	8.8	5.1	57.1	3.5	8.2	36.7	7.3	2.7	F-W
OLEACEAE									
<u>Osmanthus americanus</u> (OA)	560.5	228.1	40.7	86.1	74.1	1.5	3.1	44.0	W
<u>Chionanthus virginica</u> (CV)	1038.7	328.4	31.6	126.4	82.2	4.1	2.3	55.6	S
PALMAE									
<u>Sabal minor</u> (SM)	484.3	237.0	48.9	147.7	40.3	0.9	-	-	F-W
PHYTOLACCACEAE									
<u>Phytollacca americana</u> (PA)	318.6	8.9	26.7	42.2	81.9	1.0	9.8	38.3	F
ROSACEAE									
<u>Crataegus uniflora</u> (CRU)	771.7	30.9	20.0	135.8	78.0	1.1	1.7	37.9	F
<u>Prunus angustifolia</u> (PRA)	2503.1	287.8	11.5	254.8	88.5	1.9	1.4	45.2	S
<u>Prunus caroliniana</u> (PRC)	696.0	360.5	52.0	88.9	73.5	0.4	5.9	53.2	W
<u>Prunus serotina</u> *(PRS)	613.4	108.9	17.8	28.8	77.5	0.4	3.9	62.0	S
<u>Rubus cuneifolius</u> *(RC)	915.3	2.3	7.7	31.1	88.9	0.2	5.8	67.0	S
RUBIACEAE									
<u>Mitchella repens</u> (MR)	129.5	4.3	17.3	17.2	83.9	2.1	3.8	47.7	F-W
SYMPLOCACEAE									
<u>Symplocos tinctoria</u> (ST)	147.9	55.8	37.7	25.8	72.0	23.5	13.3	15.8	F-W
ULMACEAE									
<u>Celtis laevigata</u> (CL)	193.4	106.6	55.1	56.5	34.9	2.9	6.1	39.6	F-W
VERBENIACEAE									
<u>Callicarpa americana</u> (CA)	64.9	1.8	11.1	7.9	86.3	2.3	2.8	71.3	F
VISCACEAE									
<u>Phoradendron serotinum</u> (PS)	47.5	6.4	13.5	15.0	63.5	6.4	11.5	33.1	W
VITACEAE									
<u>Amelopsis arborea</u> (AA)	485.0	22.4	13.8	52.7	87.4	1.9	-	-	F
Parthenocissus									
<u>quinquefolia</u> (PQ)	182.3	10.8	23.6	37.9	72.8	35.9	4.8	12.1	F
<u>Vitis aestivalis</u> (VIA)	438.3	31.0	14.2	74.5	80.2	2.6	2.2	66.1	S
<u>Vitis rotundifolia</u> (VIR)	2626.7	61.1	58.1	277.1	88.8	2.5	1.6	67.3	S

*

from White and Stiles, unpub. ms. (see Methods)

APPENDIX IV. BIRD-DISPERSED PLANT SPECIES AND THE BIRDS
THAT FEED ON THEIR FRUITS AT SAN FELASCO HAMMOCK, FLORIDA.
PLANT SPECIES ABBREVIATIONS ARE DEFINED IN APPENDIX III.
BIRD SPECIES ABBREVIATIONS ARE DEFINED IN TABLE 2-2

Plant Species	Bird Species																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
AA	x																					
AS				x	x			x			x	x		x	x			x				
CA							x	x			x	x	x	x	x							
CV																						
CFL	x	x	x	x				x		x	x	x	x	x	x			x				
CFO											x	x										
CRU																						
CL	x	x	x	x		x				x							x					
EA																						
IC	x		x							x			x				x					
ID			x							x												
IG																						
IO	x		x							x			x				x					
MC							x															
MG				x							x	x						x				
MR										x			x									
MRU																						
NS	x	x	x					x		x												
OA	x			x						x												
PQ														x				x	x			
PB	x	x	x							x			x				x					
PA								x														
Total	1	8	7	0	13	2	0	7	0	5	2	0	5	3	4	2	0	5	3	4	7	1

LITERATURE CITED

- Allen, S.E. 1974. Chemical analysis of ecological materials. Wiley, New York.
- Ansley, C.C. 1952. An ecological comparison of the mesic hardwood forests of central Florida. Master's Thesis, University of Florida, Gainesville.
- Association of Official Agricultural Chemist. 1965. Official methods of analysis, 10th edition. AOAC, Washington D.C.
- Augspurger, C.K. 1983. Phenology, flowering synchrony, and fruit set of six neotropical shrubs. *Biotropica* 15:257-267.
- Baird, J.W. 1980. The selection and use of fruit by birds in an eastern forest. *Wilson Bulletin* 92:63-73.
- Bent, A.C. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. National Museum Bulletin No. 197. Washington, D.C.
- Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of populations*, ed. P.J. Den Boer, G. Gradwell, pp. 298-312. Pudoc, Washington.
- Corner, E.J.H. 1964. The life of plants. Weidenfeld and Nicolson, London, England.
- Crome, F.H. 1975. The ecology of fruit pigeons in tropical northern Queensland. *Australian Wildlife Res.* 2:155-185.
- Cruz, A. 1974. Feeding assemblages of Jamaican birds. *Condor* 76:103-107.
- Daubenmire, R. 1972. Phenology and other characteristics of tropical semideciduous forest in northwestern Costa Rica. *Journal of Ecology* 60:147-170.
- Debussche, M., J. Escarpe, and J. Lepart. 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. *Vegatatio* 48:255-266.
- Delcourt, H.R., and P.A. Delcourt. 1977. Presettlement magnolia-beech climax of the gulf coastal plain: quantitative evidence from the Appalachianicola River bluffs, north central Florida. *Ecology* 58:1085-1093.

- Delcourt, P.A., and H.R. Delcourt. 1981. Vegetation maps for eastern North America: 40,000 B.P. to the present. In *Geobotany*, ed. R.C. Romans. Plenum Press, New York.
- Denslow, J.S., and T.C. Moermond. 1982. The effect of accessibility on rates of fruit removal from tropical shrubs: an experimental study. *Oecologia* 54:170-176.
- Dohrenwend, R.E. 1978. The climate of Alachua County, Florida. IFAS Agricultural Experiment Station Bulletin 796, University of Florida, Gainesville. 22 pp.
- Dorst, J. 1962. The migrations of birds. Houghton Mifflin Co., Boston.
- Dunn, W.J. 1982. Plant communities and vascular flora of San Felasco Hammock, Alachua County, Florida. Master's Thesis, University of Florida, Gainesville.
- Foster, M.S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58:73-85.
- Frankie, G.W., H.G. Baker, and P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62:881-919.
- Frost, P.G.H. 1981. Fruit-frugivore interactions in a South African coastal dune forest. *Proc. 17th Int. Ornith. Congr.*, West Berlin.
- Gill, L.S., and F.G. Hawksworth. 1961. The mistletoes: a literature review. U.S. Department of Agriculture Technical Bulletin Number 1242, 87pp.
- Greenberg, R. 1981. Frugivory in some migrant tropical forest wood warblers. *Biotropica* 13: 215-223.
- Grinnell, J. 1897. Disgorgement among song birds. *Auk* 14:318-319.
- Harper, J.L. 1977. The population biology of plants. Academic Press, New York.
- Harper, R.M. 1905. "Hammock," "hommock," or "hummock"? *Science*, New Series 22:400-402.
- Herrera, C.M. 1981a. Are tropical fruits more rewarding to dispersers than temperate one? *American Naturalist* 118:896-907.

- Herrera, C.M. 1981b. Fruit variation and competition for dispersers in natural populations of Smilax aspera. *Oikos* 36:51-58.
- Herrera, C.M. 1982a. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63:773-785.
- Herrera, C.M. 1982b. Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions. *American Naturalist* 120:219-241.
- Herrera, C.M. 1982c. Breeding systems and dispersal-related maternal reproductive effort of southern Spanish bird-dispersed plants. *Evolution* 36:1299-1314.
- Herrera, C.M. 1984a. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs* 54:1-23.
- Herrera, C.M. 1984b. Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology* 65:609-617.
- Herrera, C.M., and P. Jordano. 1981. Prunus mahaleb and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs* 51:203-218.
- Hilty, S.L. 1980. Relative abundance of north temperate zone breeding migrants in western Colombia and their impact at fruiting trees. In *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation*. ed. A. Keast and M.S. Morton, pp.265-271. Smithsonian Inst. Press, Washington D.C.
- Howe, H.F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58:539-550.
- Howe, H.F. 1980. Monkey dispersal and waste of a neotropical fruit. *Ecology* 61:944-959.
- Howe, H.F. 1981. Dispersal of a neotropical nutmeg (Virola sebifera) by birds. *Auk* 98:88-98.
- Howe, H.F., and D. DeSteven. 1979. Fruit production, migrant bird visitation, and seed dispersal in Guarea glabra in Panama. *Oecologia* 39:185-196.
- Howe, H.F., and G.F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111:817-832.

- Howe, H.F., and R.B. Primack. 1975. Differential seed dispersal by birds of the tree Casearia nitida (Flacourtiaceae). *Biotropica* 7:278-283.
- Howe, H.F., and G.A. Vande Kerckhove. 1980. Nutmeg dispersal by tropical birds. *Science* 210:925-927.
- Howe, H.F., and G.A. Vande Kerckhove. 1981. Removal of wild nutmeg (Virola surinamensis) crops by birds. *Ecology* 62:1093-1106.
- Howe, H.F., and J. Smallwood. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13:201-228.
- Howell, A.H. 1932. Florida bird life. Coward-McAnn Inc., New York.
- Janson, C.H. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219:187-189.
- Janzen, D.H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21:620-637.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501-529.
- Janzen, D.H. 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2:465-492.
- Janzen, D.H. 1977. Why fruits rot, seeds mold, and meat spoils. *American Naturalist* 111:691-713.
- Janzen, D.H. 1983. Dispersal of seeds by vertebrate guts. in *Coevolution*, ed. D.J. Futuyma and M. Slatkin, pp 232-262. Sinauer Assoc., Sunderland, Mass.
- Johnson, R.A., M.F. Willson, J.N. Thompson, and R.I. Bertin. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* 66:819-827.
- Jordano, P. 1982. Migrant birds are the main seed dispersers of blackberries in southern Spain. *Oikos* 38:183-193.
- Jordano, P., and C.M. Herrera. 1981. The frugivorous diet of blackcap populations (Sylvia atricapilla) wintering in southern Spain. *Ibis* 123:502-507.

- Krefting, L.W. and E.I. Roe. 1949. The role of some birds and mammals in seed germination. *Ecological Monographs* 19:269-286.
- Laessle, A.M. 1958. A report of succession studies of selected plant communities on the University of Florida Conservation Preserve, Welaka, Florida. *Quart. Journal of the Florida Acad. of Sciences* 21:101-112.
- Land, H.C. 1963. A tropical feeding tree. *Wilson Bulletin* 75:199-200.
- Leck, C.F. 1969. Observations of birds exploiting a Central American fruit tree. *Wilson Bulletin* 81:264-269.
- Leck, C.F. 1972. The impact of some North American migrants at fruiting trees in Panama. *Auk* 89:843-850.
- Levey, D.J., T.C. Moermond, and J.S. Denslow. 1984. Fruit choice in neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* 65:844-850.
- Levin, D.A., and H.W. Kerster. 1974. Gene flow in seed plants. *Evolutionary Biology* 7:139-220.
- Lieberman, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. *Journal of Ecology* 70:791-806.
- Lincoln, F.C. 1939. The migration of American birds. Doubleday, Doran, and Co., Inc., New York.
- Martin, A.C., H.S. Zim, and A.L. Nelson. 1951. American wildlife and plants. Dover, New York.
- McAtee, W.L. 1947. The distribution of seeds by birds. *Amer. Midl. Nat.* 38:214-233.
- McDiarmid, R.W., R.E. Ricklefs, and M.S. Foster. 1977. Dispersal of Stemmadenia donnell-smithii (Apocynaceae) by birds. *Biotropica* 9:9-25.
- McDonnell, M.J., and E.W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109-116.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. in *Coevolution of animals and plants.*, ed. L.E. Gilbert and P.H. Raven. University of Texas Press, Austin.
- Moermond, T.C. and J.S. Denslow. 1983. Fruit choice in neotropical birds: effects of fruit type and accessibility on selectivity. *Journal of Animal Ecology* 52:407-420.

- Monk, C.D. 1965. Southern mixed hardwood forest of north central Florida. *Ecological Monographs* 35:335-354.
- Morden-Moore, A.L. and M.F. Willson. 1982. On the ecological significance of fruit color in Prunus serotina and Rubus occidentalis: field experiments. *Can. J. of Botany* 60:1554-1560.
- Morton, E.S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *American Naturalist* 107:8-22.
- Petrides, G.A. 1942. Ilex opaca as a late winter food for birds. *Auk* 59:581.
- Proctor, T. 1897. Disgorgement among song birds. *Auk* 14:412.
- Putz, F.E. 1979. Aseasonality in Malaysian tree phenology. *The Malaysian Forester* 42:1-24.
- Ridley, H.N. 1930. The dispersal of plants throughout the world. L. Reeve, Ashford, Kent, England.
- Rybczynski, R. and D.K. Riker. 1981. A temperate species-rich assemblage of migrant frugivorous birds. *Auk* 176-179.
- Schorger, A.W. 1955. The Passenger Pigeon, its natural history and extinction. Univ. Wisconsin Press, Madison.
- Sherburne, J.A. 1972. Effects of seasonal changes in the abundance and chemistry of the fleshy fruits of northeastern woody shrubs on patterns of exploitation by frugivorous birds. Ph.D. Thesis, Cornell University, Ithaca, New York.
- Smith, A.J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology* 56:19-34.
- Snow, D.W. 1962. The natural history of the Oilbird, Steatornis caripensis, in Trinidad, W.I. II. Population, breeding ecology, and food. *Zoologica* 47:199-221.
- Snow, D.W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194-202.
- Snow, D.W. 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13:1-14.
- Sorensen, A.E. 1981. Interactions between birds and fruit in a temperate woodland. *Oecologia* 50:242-249.

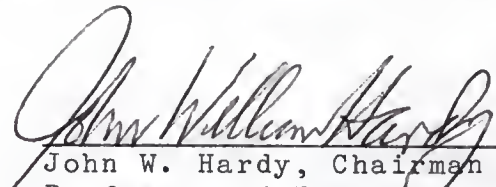
- Sorensen, A.E. 1983. Taste aversion and frugivore preference. *Oecologia* 56:117-120.
- Sorensen, A.E. 1984. Nutrition, energy, and passage time: experiments with fruit preference in European blackbirds (Turdus merula). *Journal of Animal Ecology* 53:545-557.
- Speirs, J.M. 1946. Local and migratory movements of the American Robin in eastern North America. Ph.D. Thesis, Univeristy of Illinois.
- Speirs, J.M. 1953. Winter distribution of robins east of the Rocky Mountains. *Wilson Bulletin* 65:175-183.
- Stapanian, M.A. 1982. Evolution of fruiting strategies among fleshy-fruited plant species of eastern Kansas. *Ecology* 63:1422-1431.
- Stebbins, G.L. 1970. Flowering plants: evolution above the species level. Harvard Univ. Press, Cambridge, Mass.
- Stiles, E.W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *American Naturalist* 116:670-688.
- Stiles, E.W. 1982. Fruit flags: two hypotheses. *American Naturalist* 120:500-509.
- Sutton, G.M. 1951. Dispersal of mistletoe by birds. *Wilson Bulletin* 63:235-237.
- Thompson, J.N., and M.F. Willson. 1978. Disturbance and the dispersal of fleshy fruits. *Science* 200:1161-1163.
- Thompson, J.N., and M.F. Willson. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution* 33:973-982.
- Tomlinson, P.B. 1980. Trees native to tropical Florida. Harvard University Printing Office, Cambridge, Mass.
- Turcek, F.J. 1963. Color preference in fruit and seed-eating birds. *Proc. Int. Ornith. Congr.* 13:285-292.
- Van der Pijl, L. 1972. Principles of dispersal in higher plants. Springer-Verlag, New York.
- Veno, P.A. 1976. Successional relationships of five Florida plant communities. *Ecology* 57:498-508.
- Walsberg, G.E. 1975. Digestive adaptations of Phainopepla nitens associated with the eating of mistletoe berries. *Condor* 77:169-174.

- Wetmore, A. 1914. The development of the stomach in the euphonias. *Auk* 31:458-461.
- Wheelwright, N.T. 1983. Fruits and the ecology of the Resplendent Quetzal. *Auk* 100:286-301.
- Wheelwright, N.T. In Press. The timing of flowering and fruiting in a guild of tropical bird-dispersed trees. *Oikos*.
- Wheelwright, N.T., and G.H. Orians. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist* 119:402-413.
- Wheelwright, N.T., W.A. Haber, K.G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16:173-192.
- Willis, E.O. 1966. Competitive exclusion and birds at fruiting trees in western Colombia. *Auk* 83:479-480.
- Willson, M.F., and M.N. Melampy. 1983. The effect of bicolored fruit displays on fruit removal by avian frugivores. *Oikos* 41:27-31.
- Willson, M.F., and J.N. Thompson. 1982. Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are "green." *Can. J. Bot.* 60:701-713.
- Yemm, E.W., and A.J. Willis. 1954. The estimation of carbohydrates in plant extracts by anthrone. *Biochemical Journal* 57:508-514.

BIOGRAPHICAL SKETCH

Stewart Thomas Skeate was born on the day of the Druid New Year, in 1952, in Red Bank, New Jersey. He remained in New Jersey until 1976 at which time he received his B.S. in biology from Rutgers University. Having been bitten by the biology bug, young Skeate decided to continue his education at California State University, Fullerton. Packing his 1962 VW bug with all his earthly possessions, he motored west to seek his fortune. What he found was a biological paradise in the form of desert, mountain, and coastal habitats. For the next 3 years, young Skeate chased parrots throughout Northern Mexico, receiving his master's in 1979. At this time, with visions of a Ph.D. in his head, the now older Skeate migrated back east to the lowlands of Florida to continue his graduate crusade. For the next 5 years, he roamed San Felasco Hammock State Preserve in the quest for his Ph.D. When Skeate is not working, one may find him canoeing, taking photographs, bird-watching, or at the movies.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



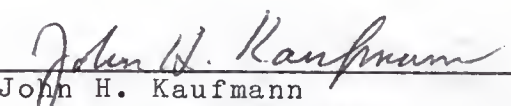
John W. Hardy, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



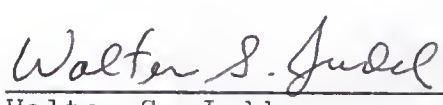
Peter Feinsinger
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



John H. Kaufmann
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Walter S. Judd
Associate Professor of Botany

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1985

Dean, Graduate School

